Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania. Part I

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Contents of Part I

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NOTE – References and Index are included in Part II.

Synopsis

A revision of the fossil bovids from Olduvai Gorge, Tanzania, is given, and they are compared with those of other published sites in East and South Africa. The new species *Syncerus acoelotus* and *Damaliscus agelaius* are described. A neotype is erected for *Megalotragus kattwinkeli* (Schwarz). In the second part of the work is an account of the bovids from each site at Olduvai. This paper covers all material brought out of the Gorge until January 1971 and some later material.

Introduction

Olduvai Gorge, formerly called Oldoway or Duwai Gorge, is famous as one of the foremost sites in the world for the remains of early man. It lies in a corner of the Serengeti Plains of northern Tanzania at 2°59′ S 35°21′ E, a little to the west of the eastern Rift Valley. The gorge runs eastwards from Lake Elgarja or Lgarya (also called Lake Ndutu) and cuts into Pleistocene beds. After about 37 km it joins up with a side gorge from the south and after another 9 km drains into the Balbal depression at the foot of the Ngorongoro–Olmoti highlands. The earliest European traveller in this part of Tanzania was Dr Oscar Baumann in March 1892 who used the name Duvai for the small hill about 15 km south-east of Lake Elgarja, but the discovery of mammalian fossils in the nearby gorge was left to Professor Kattwinkel of Munich, or perhaps Mrs Kattwinkel (Branca 1914 : 1171), in or shortly before 1911. The fossiliferous beds were explored more thoroughly in October to December 1913 by a German expedition under the leadership of Professor Hans Reck. Further expeditions were abandoned because of the outbreak of the First World War, but a series of faunal reports was initiated (Dietrich 1916, and from 1925 onwards the articles in the series entitled *Wissenschaftliche Ergebnisse der Oldoway-Expedition 1913*). The 1913 expedition found no artifacts, but had excavated a human skeleton which became the subject of a long controversy before being accepted in 1935 as an intrusive burial of *Homo sapiens*. M. D. Leakey (1971b : 225) gives a summary and further references on this important aspect of the early studies at Olduvai Gorge. Notwithstanding the ultimate verdict on the skeleton, it helped to maintain interest in the Gorge. In the late 1920s Dr L. S. B. Leakey became concerned about how to correlate his own human and faunal finds in Kenya with those at Olduvai. The human fossils were similar but the accompanying fauna was much younger than at Olduvai.

Accordingly he twice visited Professor Reck in Berlin, and eventually Reck joined his East African Archaeological Expedition of 1931–32 which worked at Olduvai. The expedition relocated the site where the human skeleton had been found 18 years earlier. Of greater interest for us today was the recovery of more fauna and the discovery that artifacts were present in all levels. Leakey did much more work at Olduvai in later years and tried to establish a sequence of stages for the evolution of the stone tool cultures. His results were presented in Leakey (1951). For a long time fossils of hominids remained scarce. Two cranial vault fragments were discovered in 1935, a hominid molar tooth and canine in 1955, and another hominid molar tooth in June 1959. Then on 17 July 1959 came the discovery by M. D. Leakey of one of the most famous skulls in African prehistory, that of the australopithecine which was later named *Zinjanthropus boisei* (Leakey 1959). Thereafter the Leakeys obtained financial support for more intensive excavations of hominid occupation sites.

It has now become clear that the Olduvai deposits span a period going back to the start of the Pleistocene. Reck (1914 : 84; *in* Leakey 1951 : 5) outlined the stratigraphy, and proposed a division into five beds numbered I, II, III, IV and V from below upwards. The first four of these beds have been found satisfactory in the subsequent geological work of R. L. Hay (1963, 1967, 1971, 1976), although he points out that in modern stratigraphical practice the beds would be considered formations. According to Hay, seven beds are present above basement rocks and together they reach a maximum exposed thickness of 100 m. The beds were laid down in a shallow basin under arid or semi-arid conditions. Bed I, of exposed thickness varying from 18 to 43 m, and the lower part of Bed II were laid down unaccompanied by much faulting and comprise the lower sequence. Many of the constituent rocks of Bed I are volcanic trachytes, clays and lava flows, and palaeosols are frequent. A shallow, saline lake occupied part of the western area of the sequence and there were lake margin and alluvial fan deposits to its east. Nearly all Bed I fossils come from east of the lake.

The onset of widespread faulting gave rise to a major depositional disconformity. Thereafter the middle and upper parts of Bed II above the Lemuta Member, itself underlying the disconformity, and Beds III and IV were laid down in an alluvial plain with a much smaller lake. There are mainly clays, sandstones and conglomerates from the start of middle Bed II upwards. The entire Bed II is 20–30 m thick, and Beds III and IV up to 45 m. Beds III and IV are distinguishable as two separate units only in the eastern part of the Gorge. On top of Bed IV are the Masek Beds, the deposition of which ceased when the subsidence of Balbal lowered the base level sufficiently to cause erosion of the Gorge.

The Ndutu Beds, constituting the older part of the former Bed V, were deposited after the Gorge had attained about three-quarters of its present depth. Following the latest known faulting in the region, these beds were themselves eroded and the Gorge cut to its present depth. The Naisiusiu Beds were laid down during the period from a little over 20 000 to 15 000 years ago.

Potassium-argon (K-Ar) studies have given a date of 1·79 million years for Tuff IB (Evernden & Curtis 1965 : 354; Curtis & Hay 1972 : 295). The same tuff gave an age of 2·03 ± 0·28 million years by the entirely independent method of fission-track dating (Fleischer, Price, Walker & Leakey 1965 : 72). Considerable overlap of K-Ar dates for the Bed I tuffs suggests a probable deposition period of as little as 130 000 years for the greater part of Bed I (Curtis & Hay 1972 : 293–294). The mean age for Bed I is 1·82 ± 0·13 million years. Dates from higher levels are more uncertain, but palaeomagnetic and other studies have been combined to produce the suggestions of 1·7 million years for the top of Bed I, 1·15 million years for the top of Bed II, 0·8 million years for the top of Bed III and 0·6 million years for the top of Bed IV (Hay 1976). Beds I to IV would thus be encompassed in that part of the Pleistocene which ended with the onset of the Mindel or Elsterian glaciation in continental Europe (Berggren & van Couvering 1974 : 92, fig. 11). They would be largely of Lower Pleistocene age.

The family Bovidae is one of the most abundant mammal groups at Olduvai. M. D. Leakey (1971b : 257, table 4) shows the numbers of bones of larger reptiles and mammals occurring at the excavated sites. In this grouping, which excludes rodents, bats and insectivores, the percentages of bovids go as high as 80·9. We calculated the mean value for the 21 bovid entries in this table as 51·8 %. Studies of the Olduvai bovids have been made previously by Reck (1928, 1935, 1937) and

Schwarz (1932, 1937), who described material in Berlin and Munich which had been collected by the expedition of 1913. This material came entirely from Beds II, III and IV; none was from Bed I. Hopwood (1934, 1936) and Leakey (1951) worked on material in London collected by the Third and Fourth East African Archaeological Expeditions of 1931–32 and 1934–35. Leakey (1965) made new identifications of some of the earlier material, and also began the descriptions of material from the new excavations. Gentry (1965, 1966, 1967) revised some of the tribal and generic assignments. Cooke (1963) compared the East African fossils with those from South African sites.

There are collections or examples of Olduvai antelopes in the Institut für Paläontologie und Museum der Math.-Naturwissenschaftlichen Fakultät der Humboldt-Universität, Berlin (the type specimen of *Pelorovis oldowayensis*), the British Museum (Natural History), London (material from the years 1931–35 inclusive), the National Museum of Kenya, Nairobi (material recovered after 1935) and the National Museum of Tanzania, Dar es Salaam. Nearly all the material formerly in the Paläontologischen Staatssammlung in Munich, which included Schwarz's (1932, 1937) type specimens, was destroyed during the Second World War. The only exceptions are the single cranium of *Thaleroceros radiciformis* and a few primates. We visited Munich in July 1969 and were assured by Professor Dr R. Dehm and Dr F. Obergfell that all the Olduvai material that survived the war has now been unpacked, and that none remains in storage. Thus nearly all of the material collected by the expedition of 1913 has been lost.

In this work we have revised the identification and classification of many Olduvai bovids, referred for the first time to much of the material excavated in the 1960s and compared the bovid fauna with that of other East African and some South African sites (see Fig. 37 in Part II of this paper). We have also made comparisons with published north African material.

Omo in southern Ethiopia, particularly the Shungura Formation, is an important comparative site. Arambourg collected there in 1932–33, and there has been a series of French and American expeditions since 1967 (see Arambourg 1941, 1947; Howell 1968; Coppens 1973). The succession consists of a basal member followed in ascending order by members A to L. Radiometric dates given by Brown (1972) include 2·16–2·56 million years for Tuff D at the base of member D and 1·81–1·87 million years for Tuff I_2 in member H. Recent palaeomagnetic work by Brown and others suggests that the formation spans the age range 3·2 to 0·9 million years and that member H correlates in time with Olduvai Bed I. Both the French and American parties and a Kenya expedition of 1967 have collected fossils from the Usno and the Mursi Formations at Omo, the former having a K-Ar date of nearly 3 million years and the latter about 4 million years.

Fossils from the Pliocene–Pleistocene beds at Kaiso, Uganda, have been revised by Cooke & Coryndon (1970) and include some bovids. They point to the existence of two faunal levels, and material from Nyabrogo and Nyawiega is thought to be earlier than that from Kaiso Village and Behanga.

In the 1930s Leakey's expeditions collected fossils from a number of localities on the southern shore of the Kavirondo Gulf, Lake Victoria. Kent (1942) mentioned Kanam East, Kanam West, Kanam Central and Kokkoth in the oldest Kanam Beds; Rawe, Fish Cliff, Kagua and probably Kanam East Hot Springs in the next oldest Rawe Beds; and Kanjera in the younger Kanjera Beds.

Expeditions to Peninj near Lake Natron, Tanzania, were organized in 1963 and 1964. The fossils, which are now in Dar es Salaam, nearly all came from the Humbu Formation which is probably contemporary with the upper part of Olduvai Bed II above the Lemuta Member (Isaac 1967 : 251). Isaac & Curtis (1974) suggest an age of the order of 1·0–1·5 million years, on the basis of palaeomagnetic data and K-Ar dating. In relation to the individual fossils mentioned in the present paper, the initials BSC refer to basal sandy clays below the Limestone and Basaltic Tuff Member, MZ to the sediments immediately above this member and USC to the upper sandy clays from there to the base of the overlying Moinik Formation.

The Laetolil area (Kent 1941; M. D. Leakey *et al.* 1976) is about 20 miles south of Olduvai close to the north-western shore of Lake Eyasi. Fossil mammals were collected from the surface of terrestrial deposits there by Kohl-Larsen in 1938–39, and by Leakey in 1935, 1959 and 1964. Kohl-Larsen's material is now in Berlin, Leakey's 1935 material in London and his 1959 and 1964 material in Nairobi. Kohl-Larsen had also collected in 1935–36 from nearby later deposits at the north end of Lake Eyasi (=Njarasa See). Dietrich (1942 : 50) wrote that the 'old fauna' of Kohl-Larsen was found in the valleys of the Vogel River, Deturi, Oldogom, Garussi, Gadjingero and Marambu. The first site of this list is Laetolil in the restricted sense and is apparently the site originally worked by Leakey (Maglio 1973 : 69). However, the 'old fauna' at all the sites is derived from the Laetolil Beds (=the Vogel River Series of Maglio 1973 : 72, *ex* Bishop). Later deposits are present in the Laetolil area, and some mixing takes place of the fossils of the old fauna with younger fossils. Maglio (1970 : 331; 1973 : 69–72) recognized at least two discrete faunal levels in the Laetolil material, one coming from the Laetolil Beds and the other dating from just before Bed I. Most bovids from the Laetolil area are unlike Olduvai species, and clearly belong to the 'old fauna' of the Laetolil Beds. M. D. Leakey *et al.* (1976) have given K-Ar dates for this fauna of between 3·59 and 3·77 million years. However, a few of the fossils collected by Leakey in 1959 are much more recent and must be coeval with or later than Olduvai. The specimens include horn cores of *Connochaetes taurinus* and a subfossil horn core of a Grant's gazelle.

We visited museums in South Africa in 1969 and 1971. In the South African Museum, Cape Town, we saw bovids from the Cape Province sites Langebaanweg, Elandsfontein (=Hopefield), Melkbos and Swartklip. In the National Museum, Bloemfontein, we saw material from Cornelia, Florisbad, Vlakkraal (=Prinsloo), Mahemspan and other Orange Free State sites, and in the Bernard Price Institute for Palaeontological Research, Johannesburg, we saw material from Makapansgat Limeworks in the Transvaal. The bovid faunas at several of these sites were reviewed by Wells (1967). The geology and fauna, including antelopes, of Melkbos and Langebaanweg were discussed in three papers by Hendey (1968, 1970a, 1970b) and of Swartklip by Hendey & Hendey (1968). The bovids from Makapansgat Limeworks have been studied by Wells & Cooke (1956) and those of Cornelia by Cooke (1974). A preliminary survey of the Langebaanweg bovids was made by Gentry (*in* Hendey 1970a), but several identifications are now known to have been incorrect. Wells (1969a) and Hendey (1969) have considered the probable age of these and other South African sites, and Hendey (1974 : 56) has based a sequence of mammal ages on them. Hendey's post-Miocene sequence and placing of the above-mentioned sites is:

Langebaanian	Langebaanweg
Makapanian	Makapansgat Limeworks
Cornelian	Cornelia, Elandsfontein
Florisian	Florisbad, Vlakkraal, Mahemspan, Melkbos, Swartklip.

Some Elandsfontein material is thought to be of Florisian age, and some Langebaanweg (Baard's Quarry) of Makapanian age. Apart from one or two specimens we did not see material from the Vaal River Gravels described by Cooke (1949), or from the following Florisian sites: Cave of Hearths and Kalkbank (Cooke *in* Mason 1962), and Wonderwerk Cave (Cooke 1941; Wells 1943).

Little radiometric dating is possible for these sites. The Peat Layer I at Florisbad, from which the fauna came, has ^{14}C dates ranging from above 35 000 to above 48 000 BP, and the Middle Stone Age levels of the Cave of Hearths from below 18 000 BP (Deacon 1966 : 27, 28). However, a new series of dates from South Africa and other lines of evidence suggest that the entire Middle Stone Age spanned a period from upwards of 100 000 until 40–30 000 BP (Beaumont 1973 : 46; Klein 1974b : 257). Consequently both Cave of Hearths and Florisbad are likely to be very much older than originally thought.

We have seen material in the British Museum (Natural History) from the middle Pleistocene site of Broken Hill, now Kabwe, Zambia (Clark 1959), and from the middle Pleistocene of the Chiwondo Beds, Malawi, reported on by Coryndon (1966).

Anatomical measurements in this paper are given in millimetres. However, geological measurements, quoted from the most recent workers at Olduvai, are given in imperial units, and we have added the metric equivalents for convenience.

Horn cores are described as obliquely inserted when their inclinations are low in side view. This is the opposite condition from having upright insertions.

We have used the designation 'upper molar' in relation to isolated teeth without trying to differentiate M^1, M^2 and M^3. However with isolated lower teeth we have specified M_3 separately, so that 'lower molar' includes only M_1 and M_2.

A basal pillar is a pillar in the centre of the medial edge of the upper molars or the lateral edge of lower molars, completely or partly separate from the rest of the occlusal surface. The upper basal pillar is the entostyle and the lower the ectostylid.

A goat fold is a transverse flange at the front of the lower molars of some bovid groups.

Measurements of length on limb bones were taken as follows:

Femur from the lateral end of the articular head to the lowest level of the distal medial condyle.

Tibia from the lowest point of the top medial facet to the projecting tip behind the medial malleolus.

Metatarsal from the highest point behind the medial part of the ectocuneiform facet to the medial side of the most projecting part of the distal medial condyle.

STRATIGRAPHY		SITES	
Naisiusiu Beds			
Ndutu Beds			
Masek Beds		FLK	
Aeolian tuff			
BED IV		GC GTC WK group PDK HEB group LK and RK	BK Bos K Hoopoe Gully VFK
		EF-HR	
BED III		JK2 GP8 JK1 JK2 JK group	
BED II	*upper* IID	BK FK West Kar K Rhino K TK	GRC MRC
	IIC	Kit K	
	middle IIB	SHK EF-HR Elephant K MNK Occupation Site FC West	Long K FLK
		MNK Skull Site HWK East levels 3-5 Sandy Conglomerate HWK EE	
	IIA Lemuta Member		
	lower IF	FLKN Clay with root casts HWK East levels 1-2 HWK FLK West	
			?FLKN Ostrich Site
BED I	ID	HWK FLKN levels 1-6	VEK KK MJTK
	IB	FLK FLKNN	
		DK THC	
Basalts of Bed I			

Fig. 1 Sites where bovids have been found at Olduvai Gorge since the Second World War, shown in relation to the stratigraphy. Some of the tuffs from IB to IID are also shown.

Humerus from the top of the lateral tuberosity to the lowest point of the medial side distally.

Radius from the centre of the medial edge of the proximal medial facet to the lowest point of the ridge on the medial side of the scaphoid facet.

Metacarpal from the edge of the proximal articular facet above the insertion for the extensor carpi radialis to the median side of the most projecting part of the distal medial condyle.

Fossils at Olduvai have been found on the surface or have been excavated from sites named according to a convention using groups of initials, e.g. BK or SHK (see M. D. Leakey *in* L. S. B. Leakey 1965 appendix 2; M. D. Leakey 1971b). Fig. 1 shows the position of many of these sites in relation to the stratigraphy of the Gorge. In this paper a specimen designation such as BK II 1953.85 means site BK in Bed II during the year 1953, specimen number 85. BK II 1963.067/1648 indicates an unnumbered specimen found in 1963 in BK II which in 1967 was given the number 1648. 068 is the prefix for similar specimens numbered in 1968. Sometimes the subdivisions of Bed II are given, e.g. FC West middle Bed II 1963.201. Material gathered from Olduvai in 1941 was given numbers prefixed by 'F', as in F.3001. In recent years single fossil finds have been given numbers prefixed by 'S', e.g. S.38, in which the initial stands for 'sundry'. The abbreviations P.P.F., P.P.R. and P.P.T. refer to short lists of figured, referred and type material in Nairobi. BM(NH) is the abbreviation for the British Museum (Natural History), KNM for the National Museum of Kenya, Nairobi, SAM for the South African Museum, Cape Town, and BPI for the Bernard Price Institute for Palaeontological Research in Johannesburg. Text references to works by L. S. B. Leakey are given as 'Leakey', and other members of his family are distinguished by their initials. Photographs of some of the best Olduvai fossils mentioned in this paper are given in Leakey (1965).

Acknowledgements

We thank Dr M. D. Leakey and the late Dr L. S. B. Leakey whose many years of work at Olduvai Gorge have made available the antelope collections which we describe. Professor H. B. S. Cooke allowed us to see unpublished papers, and Mr J. W. Simons provided information about Olduvai bovines. Professor R. L. Hay identified some matrix samples and discussed geological matters. Dr M. D. Leakey kindly read an earlier draft of this paper with great care. Professors Hay and Cooke also made helpful comments on the text. Mr R. I. M. Campbell photographed nearly all the Nairobi specimens which we wished to illustrate, and Mr J. Leonard took photographs of a few others. Dr J. van Heerden photographed the *Damaliscus niro* frontlet in Bloemfontein. We are grateful for the assistance of the staffs of the museums and institutes in Nairobi, Dar es Salaam, Cape Town, Bloemfontein, Johannesburg, Pretoria, London, Munich and Berlin.

Much of the cost of our travels in connection with this work was borne by the Wenner-Gren Foundation for Anthropological Research in New York.

Systematics

In this paper the following classification of bovids will be followed:

Family BOVIDAE	
Subfamily BOVINAE	
Tribe TRAGELAPHINI	kudus, bushbuck and related antelopes.
Tribe BOSELAPHINI	now represented by only two tragelaphine-like antelopes in India, but formerly occurring in Africa. None found at Olduvai Gorge.
Tribe BOVINI	cattle and buffaloes.
Subfamily CEPHALOPHINAE	
Tribe CEPHALOPHINI	duikers, small forest antelopes only rarely fossilized and not found at Olduvai Gorge.

Subfamily HIPPOTRAGINAE	
Tribe REDUNCINI	reedbucks, kob, lechwes and waterbuck.
Tribe HIPPOTRAGINI	roan, sable, oryxes and addax.
Subfamily ALCELAPHINAE	
Tribe ALCELAPHINI	wildebeest and hartebeest group, impala.
Subfamily ANTILOPINAE	
Tribe NEOTRAGINI	dik dik and other small antelopes.
Tribe ANTILOPINI [incl. Saigini]	gazelles, springbok.
Subfamily CAPRINAE	
Tribe 'RUPICAPRINI'	goral and serow group, not found in Africa. (*Rupicapra* itself might be better placed in the Caprini.)
Tribe OVIBOVINI	muskox, takin and extinct allied forms.
Tribe CAPRINI	sheep and goats.

More detailed information will be found under the tribal headings.

Tragelaphines are rare at Olduvai except for two temporal subspecies of the greater kudu. Two lineages of Bovini, two of Reduncini and an extinct *Hippotragus* are moderately common. The Alcelaphini and an extinct springbok are well represented at the Gorge. A number of other forms occur as rarities.

Tribe **TRAGELAPHINI**

Living members of the tribe are the sitatunga, bushbuck, greater and lesser kudus, nyala, mountain nyala and bongo which are all placed in the genus *Tragelaphus*, and the eland placed in *Taurotragus*. They are medium to large antelopes with spiralled horns and rather brachyodont teeth, which live where there is cover or even forest and feed mainly by selective browsing. Their characteristic skull features are: horn cores keeled, spiralled (torsion anticlockwise from the base upwards on the right side), inserted obliquely and behind the orbits. Frontals between the horn core bases slightly raised above the level of the top of the orbital rims, braincase little angled on the facial axis and sometimes widening posteriorly in dorsal view, side wall of the braincase with a depression below and behind each horn core base, no postcornual fossae, the front of the orbit tending to lack a rim along the lachrymal edge, nasals long and narrow, ethmoidal fissures large, no preorbital fossae, infraorbital foramen low over the tooth row and anteriorly placed, premaxillae rising as far as the nasals in side view and narrowing anteriorly to a blunt end in ventral view, occipital surface tending to be flattened, mastoids small, basioccipital long with a central transverse constriction and anterior tuberosities passing in front of the level of the foramina ovalia. Teeth rather brachyodont, basal pillars small or absent on lower molars and absent on upper molars, central cavities without a complicated outline, upper molars without prominently outbowed ribs between the styles, lower molars with narrowly pointed lateral lobes and without goat folds, premolar rows long and P2s large, P_4s often with paraconid–metaconid fusion which closes the anterior part of the medial wall, and mandibles with shallow horizontal rami.

Tragelaphus scriptus (Pallas 1766), the bushbuck, was once common in most of Africa south of the Sahara, living mainly in bush or lightly wooded country. It is small to medium-sized and has anteroposteriorly compressed horn cores with the posterolateral keel the main one.

Tragelaphus spekei P. L. Sclater 1864, the sitatunga, lives in swamps in parts of Africa as far south as the extreme north-east of Namibia (South West Africa). It is medium-sized and has long hoofs and longer horns than in the smaller bushbuck.

Tragelaphus angasi Gray 1849, the nyala, is medium-sized and found in woodlands with thickets in restricted parts of south-east Africa. The males have manes along the top of the back and on the centre of belly and neck.

Tragelaphus imberbis (Blyth 1869), the lesser kudu, usually occurs in rather dense thickets in bush-covered desert in parts of east Africa from Somalia southwards. It may also occur in Arabia (Harrison 1972 : 629). It is medium-sized and has horn cores differing rather indistinctly from those of the sitatunga by being longer, more spiralled, less divergent, and with a less strong posterolateral keel.

Tragelaphus strepsiceros (Pallas 1766), the greater kudu, is absent from north and west Africa. It is a large antelope and has large and strongly spiralled horn cores with an anterior keel and no anteroposterior compression. It lives in hilly country and thickets, even in fairly arid country.

Tragelaphus buxtoni (Lydekker 1910), the mountain nyala, is endemic to the Ethiopian highlands east of the Rift Valley, living in forests, heath and grasslands around 3000–3500 m. It is medium-sized to large and in some features of its horn cores resembles the greater kudu.

Tragelaphus eurycerus (Ogilby 1837), the bongo, is discontinuously distributed in thick forest of west Africa, Zaïre (Congo) and east Africa. It is large and short-legged and both sexes have horns.

Taurotragus oryx (Pallas 1766), the eland, is the largest tragelaphine and occurs in much of Africa south of the Sahara. It has horn cores in both sexes with a strong anterior keel, without anteroposterior compression, quite tightly twisted about their axes but less openly spiralled than in any other tragelaphine. It avoids dense cover but otherwise is found in a wide range of habitats like the greater kudu.

Genus *TRAGELAPHUS* Blainville 1816

TYPE SPECIES. *Tragelaphus scriptus* (Pallas 1766).

GENERIC DIAGNOSIS. Medium to large tragelaphines with spiralled horn cores inserted close together and having an anterior keel and sometimes a strong posterolateral one; small to medium-sized supraorbital pits, which are frequently long and narrow; occipital surface tending to have a flat top edge and straight sides.

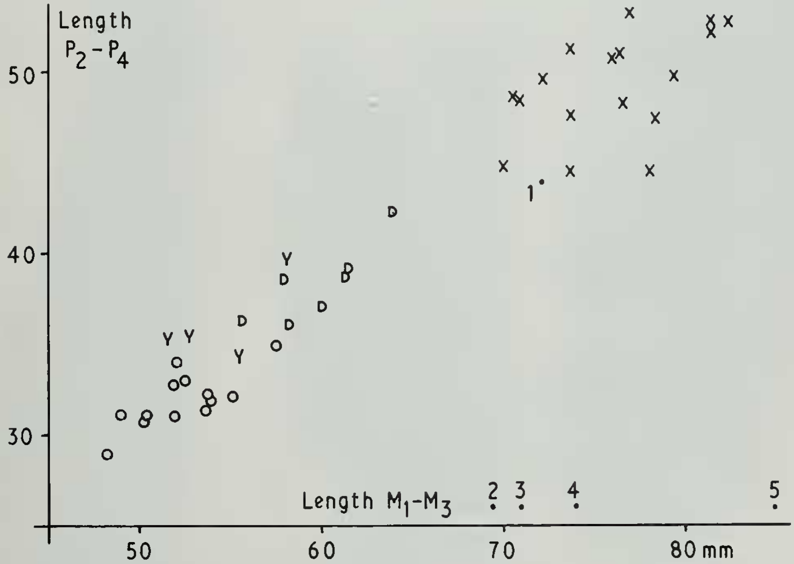

Fig. 2 Length of lower premolar row plotted against length of lower molar row for some tragelaphines.

X = Recent *Tragelaphus strepsiceros*, D = *T. imberbis*, Y = *T. angasi*, O = *T. spekei*, I = *T. strepsiceros maryanus* FLK I 067/1100.

Molar row lengths are also shown for the following: 2 = FLKN I 882, 3 = FLKNN I 66+548, 4 = DK I 3001, 5 = Peninj A67.270+A67.277. 2, 3 and 4 are *T. s. maryanus*, while 5 is probably *T. s. grandis*.

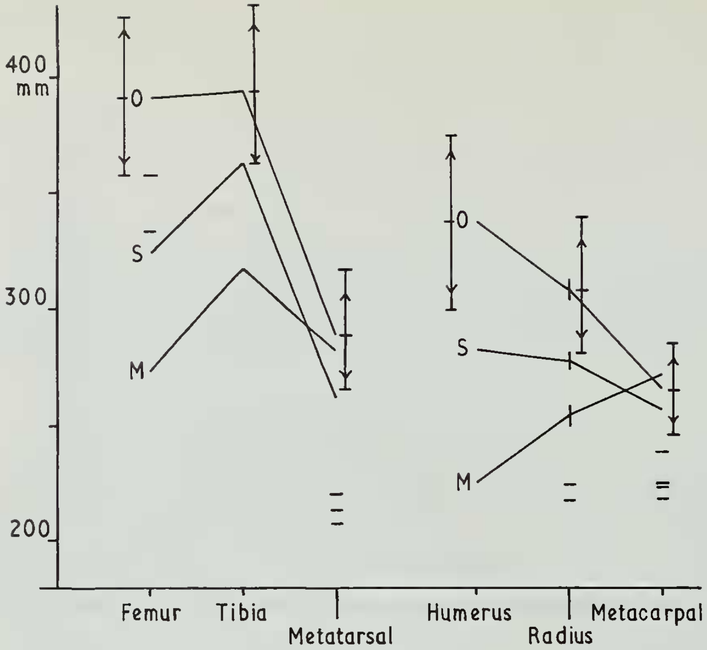

Fig. 3 Lengths of limb bones in Tragelaphini.

O = mean of 9 *Taurotragus oryx*, with vertical lines showing ranges and standard deviations. S = mean of 3 Recent *Tragelaphus strepsiceros*. M = mean of 3 *T. imberbis*.

Horizontal dashes indicate Tragelaphini from Olduvai, all from Bed I except the larger of the femora, which is from BK II. The BK II femur is probably *Tragelaphus strepsiceros grandis*, the Bed I femur has not been identified and the other limb bones are smaller than would be expected for *T. s. maryanus*.

Tragelaphus strepsiceros (Pallas 1766)

Diagnosis. A large species of *Tragelaphus* with strongly and openly spiralled horn cores, anterior keel present but posterolateral keel reduced and tending to be present only distally; compared with other *Tragelaphus* species the horn cores are more uprightly inserted and are not anteroposteriorly compressed; braincase short; a low occipital.

Tragelaphus strepsiceros maryanus (L. S. B. Leakey 1965)

1965 *Strepsiceros maryanus* Leakey : 40, pls 40–42.

Diagnosis. A subspecies of *Tragelaphus strepsiceros* differing from the living greater kudu in having horn cores with more mediolateral compression, the braincase top more angled on the facial axis, and fusion of paraconid with metaconid on all known P_4s.

Holotype. A cranium with almost complete horn cores found in 1959 and now in Dar es Salaam.

Horizon. The holotype came from level 2 of HWK East, lower Bed II, Olduvai (Leakey 1965 : 41; M. D. Leakey, personal communication) although it is inscribed 'Olduvai 1959 EKK *Strepsiceros maryanus* TYPE'. Other specimens are moderately common in Bed I, lower Bed II and perhaps early in middle Bed II.

Remarks. A frontlet of *Tragelaphus strepsiceros maryanus* with nearly complete horn cores, dentitions and partial skeleton came from FLKNN I in 1960, and a cranium 068/5813 from KK II in 1959. (Leakey states (1965 : 42) that both specimens came from Bed I.) The latter has a very strongly inclined top of its braincase. Dentitions assigned to *T. s. maryanus* are slightly smaller

1

2

3

4

Plate 1 (Scale = 25 mm)

Occlusal views of dentitions.

Fig. 1 ***Tragelaphus strepsiceros maryanus.*** Right mandible with P_2–M_3, FLK I G.067/1100.

Fig. 2 ***Tragelaphus strepsiceros maryanus.*** Left M^1–M^3 from palate, FLK I C.067/1083.

Fig. 3 ***Syncerus acoelotus.*** Left M^1–M^3, BK II 1963.2757.

Fig. 4 ***Syncerus acoelotus.*** Right mandible with P_3–M_3, BK II 1953.067/5230.

than in the living greater kudu, and a complete right lower dentition FLK I G.067/1100 also differs in having rather a short premolar row (Fig. 2; Pl. 1, fig. 1). Since this character is known from only one specimen we have not included it in the subspecific diagnosis. The paraconid–metaconid fusion on P_4 is known from five *T. s. maryanus* (two in late wear) and is just beginning on a further two in middle wear. This contrasts with its occurrence in only 13 out of 24 extant greater kudus and 3 out of 7 lesser kudus. Part of a right maxilla HWK EE II 1972.3916 has preserved its M^2 and M^3, the former having an occlusal length of 21·9 mm. This fits *T. s. maryanus* but is rather small for later greater kudus. If it is really *T. s. maryanus* then the range of the subspecies extends into lower middle Bed II.

Most of the tragelaphine limb bones from Bed I seem too small to belong to *T. s. maryanus* (Fig. 3). However, no other tragelaphine is known by cranial and dental remains and the alternative supposition that the postcranial remains alone represent another species is also hard to accept. The limb bones are discussed further in the account of the FLKNN I site.

Olduvai kudu specimens in London include three pieces possibly of *T. s. maryanus*. They are part of a right horn core M 21478 found in Bed I or II in 1947, the distal part of a left horn core M 21483, and the base of a left horn core M 21485.

MEASUREMENTS. Measurements on crania of *T. s. maryanus* are:

	Holotype	KK 068/5813
Anteroposterior diameter at base of horn core	76·5	73·7
Mediolateral diameter at base of horn core.	55·4	56·9
Minimum width across lateral surfaces of horn pedicels	*c.* 119·0	–
Maximum braincase width	119·7	122·0
Skull width across mastoids immediately behind external auditory meati .	*c.* 150·0	150·0
Occipital height from top of foramen magnum to top of occipital crest . .	58·6	58·7
Width across anterior tuberosities of basioccipital	36·4	–
Width across posterior tuberosities of basioccipital	54·2	61·0

Measurements on maxillae assigned to *T. s. maryanus* are:

	DK I 802	FLKNN I 553	FLK I C.067/1083
Occlusal length M^1–M^3	65·5	66·2	70·8
Occlusal length M^2	23·7	22·1	24·3
Occlusal length P^2–P^4	–	46·8	–

An immature maxilla FLK I G.067/1089 has deciduous P^2–P^4 at 50.0 mm.

Measurements on mandibles assigned to *T. s. maryanus* are:

	DK I 36	DK I 3001	FLKNN I 66+548	FLKNN I 62	FLK I G.067/1100	FLKN I 882
Occlusal length M_1–M_3	72·7	74·0	70·9	–	72·1	69·4
Occlusal length M_2	23·1	22·3	21·5	–	22·8	23·3
Occlusal length P_2–P_4	–	–	–	42·9	43·9	–

An immature mandible FLK I G.067/1085 has deciduous P_2–P_4 measuring 46·1 mm. It belongs to the same individual as immature maxilla G.067/1089. Maxilla FLKNN I 553 and mandibles 62 and 66 + 548 belong to one individual.

Measurements of length and least thickness on the limb bones, which are rather small for *T. s. maryanus*, using the reference points given in the introduction, are:

Metatarsals	DK I 4429	213 × 20·5	FLK I G.067/959	207 × 20·5	FLKN I 7333	220 × 25·6
Radii	FLKN I 8275	217 × 28·8	FLKN I 9290	224 × –		
Metacarpals	DK I 4141	218 × 21·8	FLKNN I 895	224 × 25·0	FLKN I 9269	223 × 23·0
	FLKN I 067/1073	222 × 25·3				

Measurements on two limb bones of a larger tragelaphine are:

Femur	DK I 5400	330 × 33·5	Metacarpal	FLK I G.258	238 × 29·0

COMPARISONS. Other fossil kudus are considered under *Tragelaphus strepsiceros grandis*, p. 303. The subspecies *T. s. maryanus* has not been discovered at any site other than Olduvai.

Tragelaphus strepsiceros grandis (L. S. B. Leakey 1965)

1965 *Strepsiceros grandis* Leakey : 38, pls 38–39.

DIAGNOSIS. A subspecies of *Tragelaphus strepsiceros* differing from the living greater kudu in its greater size; horn cores with greater basal divergence, less mediolateral compression and a more triangular cross-section; braincase widening towards the rear in dorsal view. It differs from *T. s. maryanus* by its larger size and in having horn cores with a more triangular cross-section and less mediolateral compression.

HOLOTYPE. A cranium with complete horn cores, BM(NH) M 21461, found in 1931.

HORIZON. The holotype is from upper Bed II. It came from RK (M. D. Leakey 1971b : 284). Other specimens are from middle Bed II to Bed IV at Olduvai, and from Peninj, but it is not abundant.

REMARKS. The holotype cranium is larger than large skulls of living greater kudu. Both its horn cores are complete and have strong anterior keels. Both horn cores show marks of the grubs of a moth allied to or identical with the living *Ceratophaga vastella* along the whole of their length[1].

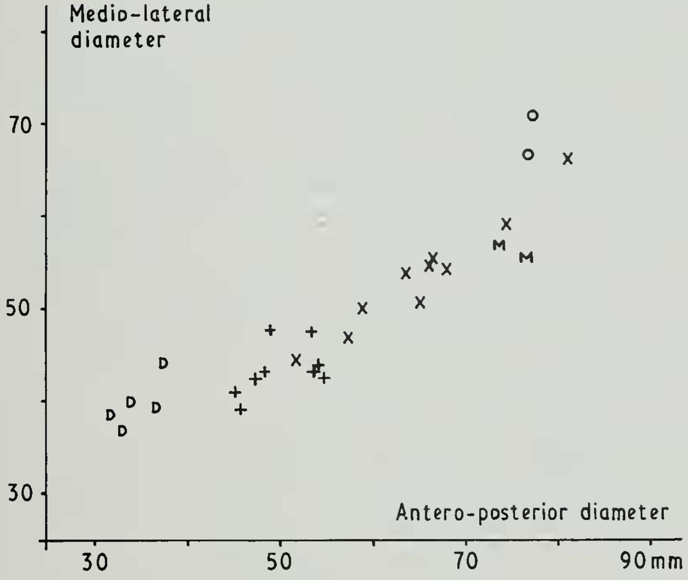

Fig. 4 Horn core dimensions of kudus.

O = *Tragelaphus strepsiceros grandis* from Olduvai Gorge, M = *T. s. maryanus* from Olduvai Gorge, + = *T. gaudryi* from member G of the Shungura Formation, X = living *T. strepsiceros*, D = *T. imberbis*.

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[1] A number of Olduvai fossil horn cores show grooves similar to those on dead modern antelopes made by grubs of the moth *Ceratophaga vastella* (Zeller) of the family Tineidae. The grubs feed on the keratin of the horn sheaths, having entered the space between the sheath and core at the base of the horn. They finally bore through the sheath to pupate in tubes of silk and detritus projecting from the sheath's external surface (Spinage 1962 : 81; pl. 36). In hot and dry regions the tubes form on the unexposed side of the horn sheath, making 'roots' into the ground (R. H. Carcasson, personal communication). Fossils showing signs of the grubs must have been lying in the open, neither buried nor under water, for a short period prior to fossilization. Leakey (1965 : 39, 51 and 62) has attributed some examples of such grooves to the gnawings of large rodents.

The fossil differs from living greater kudu in having horn cores that are set widely apart, more divergent immediately at the base in anterior view, with less emphasized spiralling, and with a less reduced posterolateral keel giving the horn core a more triangular and less oval cross-section and hence less mediolateral compression (Fig. 4). It also has a shorter, wider and relatively lower cranium, posterior widening of the braincase in dorsal view and possibly a deeper depression in the side of the braincase which is visible on the right side only. Most of these differences are likely to arise from individual variation and allometry. It is probable that the large size of *T. s. grandis* produces a general widening of the skull and enlarging of the horn cores, but the width across the supraorbital pits does not seem to be affected (Fig. 5). We consider it only subspecifically distinct from the living greater kudu. The right maxilla of the holotype is preserved separately from the cranium and has a tooth row which is larger than in most greater kudus, despite being fairly well worn.

Kudu remains in London which could be *T. s. grandis* are part of a left horn core M 21476, part of a left horn core M 21477 from BK IV found in 1935, the base of a strongly divergent left horn core M 14549 found in 1932 in Bed I (according to its label), Bed II (written on the horn core and in the register) or the surface of Bed III (Leakey 1965 : 40), and parts of right horn cores M 21469 (said by Leakey 1965 : 40 to come from the surface of CK IV in 1935), M 21470 and M 21471. The distal part of a left horn core M 14517 found in 1931 in Bed I, a small part of a left horn core M 21479, part of a horn core M 21480 found in 1931, and part of a right horn core M 21481 are all of kudus but are too fragmentary to be assigned to a subspecies. Parts of left horn cores M 14543 from Bed I and M 21482 may belong to a kudu or to a sitatunga-like tragelaphine.

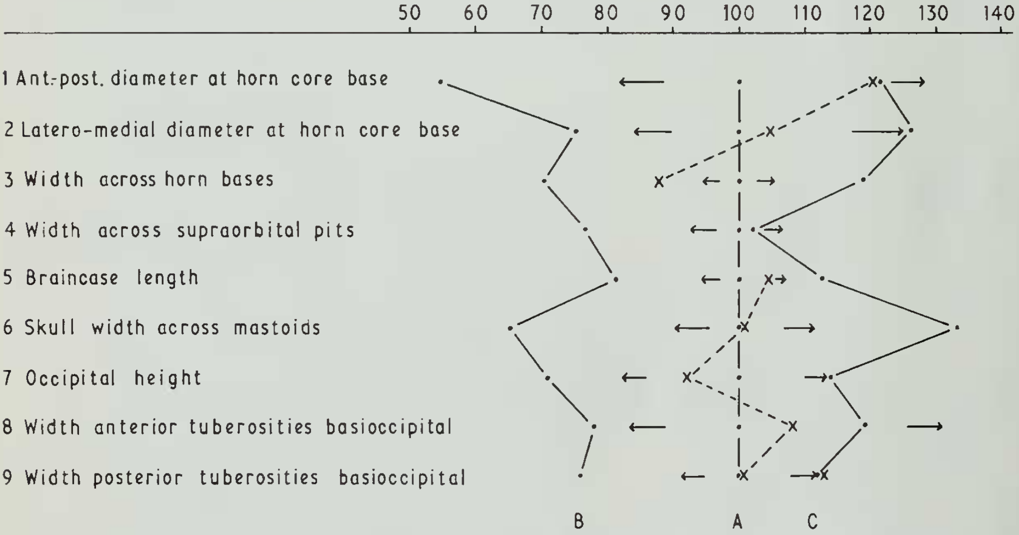

Fig. 5 Percentage diagram of skull measurements in kudus. Line A is the standard line at 100% ; readings on other lines are expressed as percentages of their values on line A.

A = mean readings for 10 adult males of living *Tragelaphus strepsiceros*, B = mean readings for 6 adult male *T. imberbis*, C = holotype of *T. strepsiceros grandis*, dashed line = holotype of *T. s. maryanus*.

Horizontal arrows show the standard deviations for line A. Braincase length is measured from the midfrontals' suture at the level of the supraorbital pits to the occipital top. *T. s. grandis* differs from the living greater kudu by being larger and having large horn cores set widely apart and a relatively low and wide occipital surface. *T. s. maryanus* shows strong mediolateral compression of the horn cores, which is probably responsible for the low reading of width across the horn bases. The relatively long and high cranium of the lesser kudu, B, is probably an effect of allometry, and this species also has mediolaterally wide horn cores.

T. strepsiceros subsp. Schwarz (1937 : 30) at Olduvai was based on a poorly-preserved frontal with horn cores which was unfortunately destroyed in Munich during the Second World War. Schwarz did not figure the specimen.

MEASUREMENTS. Measurements on the cranium and maxilla of BM(NH) M 21461 are:

Length of horn core along its front edge	*c.* 730·0
Anteroposterior diameter of horn core at its base	76·9
Mediolateral diameter of horn core at its base	66·6
Minimum width across lateral surfaces of horn core pedicels	161·0
Width across lateral edges of supraorbital pits	69·3
Maximum braincase width	135.5
Skull width across mastoids immediately behind external auditory meati	198·0
Occipital height from top of foramen magnum to top of occipital crest	72·5
Width across anterior tuberosities of basioccipital	40·0
Width across posterior tuberosities of basioccipital	60·5
Occlusal length M^1–M^3	81·7
Occlusal length M^2	*c.* 28·0
Occlusal length P^2–P^4	*c.* 50·0

COMPARISONS. A kudu-sized tragelaphine is represented at Peninj by fragments of two left maxillae A67.276 (WN 64.70 MMG.BSC) and A67.275 (WN 64.98 MMG.BSC), two pieces of a right mandible with P_4–M_3 A67.270 + A67.277 (WN 64.91 LMG.BSC.OG), the proximal end of a right metatarsal A67.346 (WN 64.420) and possibly some other pieces. We no longer believe that more than one tragelaphine is present (cf. Gentry *in* Isaac 1967 : 252). By the length of the mandibular molar row it agrees best in size with *T. s. grandis*, being a little small for an eland but rather too large for a living greater kudu.

The base of a right horn core from Kagua, BM(NH) M 15874, apparently the basis for Hopwood's (*in* Kent 1942 : 124) identification of *Taurotragus oryx*, is actually *Tragelaphus strepsiceros*. With basal diameters of 70·5 and 61·1 mm it has insufficient mediolateral compression to fit *T. s. maryanus*. It lacks the posterolateral basal keel of *T. s. grandis*. M 15884 is a small part of a kudu horn core from Kanam West. A tragelaphine left lower molar from Kanam Central, M 15933, is the size of a kudu.

A piece of horn core from the Shungura Formation, L.627-17 from member G, appears from its large size to belong to *T. strepsiceros* and is the only definite record of this species in the formation. Another kudu is common in members E to G, and was referred to *T. imberbis*, the lesser kudu, by Arambourg (1947 : 432; pl. 30, fig. 6). Its affinities are interesting. It differs from Olduvai *T. s. maryanus* and the living greater kudu by its smaller size and in having horn cores spiralled more closely to the longitudinal axis, less mediolaterally compressed at the base, less divergent overall and less uprightly inserted, braincase not widening posteriorly, and occipital surface perhaps less low and wide. The bending of the braincase on the face axis is about as strong as in *T.s. maryanus*. Passing from members E to G the anterior keel becomes stronger, the posterolateral keel weaker and mediolateral compression increases. These are all trends towards *T. strepsiceros* and away from *T. imberbis*, but the Omo kudu is unlikely to be ancestral to the Olduvai kudus. A change to *T. s. maryanus* would involve mainly a size increase with the associated changes of shortening and widening the braincase and the horn core insertions becoming more upright. However, the time margins are barely adequate according to the K-Ar dates of about 1·8 million years for Shungura tuff I_2 and about 1·9 million years for the Bed I basalts at Olduvai. *T. strepsiceros* must also have been a separate lineage, since the horn core L.627-17 occurs in the same level of member G (unit 13) as the highest horn cores of the other kudu. A cranium from Shungura member C, Omo 18 68-303, differs from the member E–G material by its slightly larger size, the weaker spiralling of its horn cores, their greater anteroposterior compression and a stronger posterolateral keel, all of which are satisfactory as ancestral character states. However, it also differs in the greater divergence of its horn cores, so that for this character it is the earlier rather than the later Shungura form which is most like *T. strepsiceros*. It is apparent that the member C cranium must be near the ancestry of both living kudus. We suggest that *T. strepsiceros* evolved from a form something like the member C cranium, but which is largely unrepresented in the Shungura Formation, and that the member E–G kudu also evolved from it. The Shungura E–G form lessened the divergence of its horn cores and perhaps diminished in size, but otherwise continued to evolve towards a *T. strepsiceros*-like morphology. By level 13 of member G, *T. strepsiceros* had appeared or reappeared in the Omo area, as witnessed by the horn core L.627-17, and we hypothesize that the Shungura kudu might then have reversed its remaining evolutionary parallels with *T. strepsiceros* and evolved into the living *T. imberbis*. Tragelaphine teeth of appropriate size for this lineage occur in higher member G and in member H, but as yet there are no horn cores. The chief motives for accepting this story are that *T. imberbis* and the Shungura species are similar-sized kudus occurring in the same region of Africa, the living one with no other known ancestor and the fossil one with no other known descendant. The outstanding interest of the story would lie in the implication that competition with a 'sister species' had led to the reacquisition of some ancestral horn core characters. Why should the species have benefited, or perhaps even been enabled to survive, by doing this?

Palaeoreas gaudryi Thomas (1884 : 15; pl. 1, fig. 7) was founded on a right horn core base (wrongly illustrated as a left) of a kudu from Ain Jourdel, an Algerian site of 'Villafranchian' (=Pliocene) age (Arambourg 1970 : 8). Joleaud (1936 : 1184) mistakenly referred *P. gaudryi* to *Taurotragus*. The horn core has an anterior keel and anteroposterior and mediolateral basal diameters of 48·8 and 47·4 mm. It is too small and has insufficient mediolateral compression for *T. s. maryanus*, but agrees with the Shungura E–G kudu in size, compression and inclination. Accordingly the latter can be referred to *Tragelaphus gaudryi* (Thomas) for the present, but it may be that the cladistic position of the Algerian form lies between the Omo member C cranium and *T. strepsiceros*. The type species of *Palaeoreas* is a small Miocene ovibovine (Gentry 1971 : 289) unconnected with the north African horn core. Another 'Villafranchian' kudu is a frontlet from Mansoura near Constantine, Algeria (Gervais 1867–69 : 92, 94; pl. 19, fig. 4), which is probably conspecific with the earlier Ain Jourdel horn core. Its spiralling lies fairly close to the longitudinal axis of the horn core, as in the Shungura kudu.

Horn cores of what appears to be a still earlier kudu occur in the Mursi Formation, Ethiopia (YS 4-4, 4-6, 4-10, YS 68-2078), and in the Karmosit beds in the Baringo area, Kenya (KNM-KM 13). They are more anteroposteriorly compressed and have a sharper posterolateral keel than in the Shungura E–G kudu, and these characters can be accepted as primitive. The horn cores agree with kudus in their increasing divergence from the base, which means that quite small pieces from any part of the horn core have the posterolateral keel along the concave edge of the curvature instead of the convex edge. This is in contrast to known members of other *Tragelaphus* lineages, but it would be premature to assume that such an early species can be related only to kudus.

The main features of skull evolution in the greater kudu can thus be taken as increasing mediolateral compression of the horn cores, increasing prominence of the anterior instead of the posterolateral keel and the horn core insertions becoming more upright. Connected with the overall increase of size, there was a shortening and widening of the braincase, and its roof acquired a less pronounced slope. The common kudu of the Shungura Formation is not an ancestor, and difficulties with *T. s. maryanus* are presented by the short premolar row of the only complete kudu-sized dentition from Bed I and by the greater proportion of P_4s with fused paraconid and metaconid than in living kudus.

Tragelaphus strepsiceros is represented by parts of two right horn cores, BM(NH) M 12147 and M 12904, at Broken Hill, Zambia, as noted by Leakey (*in* Clark 1959 : 229).

Fossil kudus are known from South African sites. At Makapansgat Limeworks, three tragelaphine species (other than the eland represented by maxilla BPI M.7) can be separated by the size of their teeth. The largest size group would correspond to larger examples of greater kudu and has been designated *Strepsiceros* cf. *strepsiceros* by Wells & Cooke (1956 : 9). It is represented by right maxillae BPI M.2 and M.3, left mandibles M.6446 and M.6690, immature right maxilla M.576 and immature left mandible M.4. More material is needed before deciding whether this tragelaphine might be *T. s. grandis*.

Remains of a distinctive extinct kudu occur at Melkbos and Elandsfontein, the Melkbos material having already been referred to by Hendey (1968 : 108). The horn cores of this species agree more with the greater than with the lesser kudu, but the spiralling is much tighter. The fossils perhaps represent a Cape species completely unknown in East Africa.

We now consider that the two pieces of horn core L.4615 and L.6586 from Langebaanweg which were recorded as a kudu by Gentry (*in* Hendey 1970a : 114) are more likely to be bovine.

Tragelaphus aff. *scriptus* (Pallas 1766)

There is some evidence for a bushbuck-like antelope at Olduvai. The distal end of a left horn core BM(NH) M 14568 from Bed IV (according to the register and by its colour; 'Bed I' on its label must be mistaken) is about the size of large horn cores of the living bushbuck, is anteroposteriorly compressed to the right extent and has an anterior keel and marked posterolateral keel. The anterior keel, however, is sharper than in most living *T. scriptus*. The distal end of a left tibia from SHK II, 1957.474 in Nairobi, is from a bushbuck-sized tragelaphine.

The frontal with horn cores called *T. scriptus* subsp. by Schwarz (1937 : 26) was destroyed in Munich in the Second World War. The specimen was not figured.

COMPARISONS. A pair of bushbuck-sized tragelaphine horn cores, L144-1 and 2 from member C of the Shungura Formation, Omo, is extremely interesting in that the horn cores are less anteroposteriorly compressed, less obliquely inclined in side view and possibly inserted less far behind the orbits than in the living bushbuck. The Makapansgat Limeworks dentitions assigned to *Cephalophus pricei* by Wells & Cooke (1956 : 12, fig. 5) belong to a bushbuck-sized tragelaphine.

Tragelaphus aff. *spekei* Sclater 1864

A skull with horn core from Olduvai was named *Tragelaphus spekei stromeri* by Schwarz (1932 : 2; 1937 : 28). It was formerly housed in Munich, but was lost during the Second World War. Schwarz described the horn core insertion as being further forward on the skull than in the living sitatunga, above the orbit instead of just behind, but did not figure the specimen. The anterior keel of the horn core was very marked. Parts of left horn cores, BM(NH) M 14543 from Bed I and M 21482, may belong either to a kudu or to a sitatunga-like antelope. The anterior keel is well marked on M 14543, which may be from near the distal end, but not on M 21482. There is no further evidence for a sitatunga at Olduvai, and we shall abandon the use of the name *T. spekei stromeri*.

COMPARISONS. Other fossils of sitatunga size are known from other African sites. The badly preserved cranium of *Tragelaphus* sp. cf. *buxtoni* from Laetolil (Dietrich 1942 : 118; pl. 19, fig. 154) was thought to have come from the early fauna, but this is not so (M. D. Leakey *et al.* 1976 : 463, 464). The rather open spiralling of its horn cores is the only reason for linking it with the living *T. buxtoni*; the oblique insertion of the horn cores is unlike *T. buxtoni*, and either *T.* sp. cf. *spekei* or *T.* sp. cf. *angasi* would have been better designations. Its horn cores are somewhat anteroposteriorly compressed, a posterolateral keel but not an anterior one is present, and the frontals are uparched between the horn core bases. Dietrich (1950 : 43) referred to another sitatunga- or nyala-sized horn core from Laetolil and to an appropriately-sized mandible.

BM(NH) M 26402 is a right horn core from the earlier fauna of the Kaiso Formation at North Nyabrogo described by Cooke & Coryndon (1970 : 200) as *Strepsiceros* cf. *maryanus*, but better identified as *Tragelaphus* sp. cf. *spekei*. It is less tightly twisted and a little less anteroposteriorly compressed than in *T. spekei*, but does not seem very primitive for its great age. It is unlikely to be a kudu because of the strong posterolateral keel, absence of an anterior keel at least lower down and the poor degree of twisting. Part of a left horn core from Kanam East M 15907 is also less anteroposteriorly compressed than in *T. spekei*. Part of a left horn core from Kanam East Hot Springs M 15929 is similar but has a stronger anterior keel. Part of a left mandible with M_2 and M_3, M 15924 from Kanam East, is too large for a bushbuck and shows larger basal pillars than in living Tragelaphini. A right mandible from Rawe M 15938 is the size of *T. spekei*. Three horn core pieces from Kanjera M 15852 (*Tragelaphus* sp. of Hopwood *in* Kent 1942 : 126) are also of sitatunga size and closer to the living species; they have poor or absent anterior keels. The base of a tragelaphine right horn core BPI M.490 and possibly a fragment M.491 from Makapansgat Limeworks show rather less anteroposterior compression than in the Kaiso horn core. Some dentitions of appropriate size to go with them have already been assigned to *T.* cf. *angasi* by Wells & Cooke (1956: 10). These are right maxilla M.5, right mandible M.6606, left mandible M.6, right M_2+M_3 M.183, left M_3s M.185 and M.186, and probably right maxilla M.1319. Very similar remains are fairly common in the Langebaanweg collection.

Genus ***TAUROTRAGUS*** Wagner 1855

Type species. *Taurotragus oryx* (Pallas 1766).

Generic diagnosis. Large tragelaphines. Compared with *Tragelaphus* the horn cores are tightly twisted and less openly spiralled, inserted wider apart, and with a strong anterior keel and sometimes a posterolateral one. Large supraorbital pits; pronounced lateral flanges at the front of the nasals; median indentation at the back of the palate passing far forwards of the lateral ones; tooth rows set more anteriorly than in *Tragelaphus*; P_4s with fused paraconid and metaconid (unfused in only 2 out of 27 *Taurotragus oryx*).

Taurotragus arkelli L. S. B. Leakey 1965

1965 *Taurotragus arkelli* Leakey: 43, pls 43 and 44.

Diagnosis. A species of *Taurotragus* differing from living *T. oryx* in having horn cores inserted less obliquely in side view, braincase top longer, cranium high and narrower, and the braincase top not depressed to produce a transverse crest across the top of the occipital.

Holotype. Cranium with complete left and basal half of the right horn core, F.3665 P.P.T.4 found in 1941. At present in the Nairobi collections.

Horizon. The holotype was found on the surface of Bed IV, between LK and RK. Apart from this the eland is poorly represented at Olduvai.

Remarks. The single cranium of *T. arkelli* is a little smaller than crania of the living eland and the horn cores are inserted less obliquely and perhaps closer to the orbits. The supraorbital pits are rather close together. Other differences from living *T. oryx* are connected with the less oblique insertions of the horn cores; these are the longer braincase top (Fig. 6), no temporal fossa, and

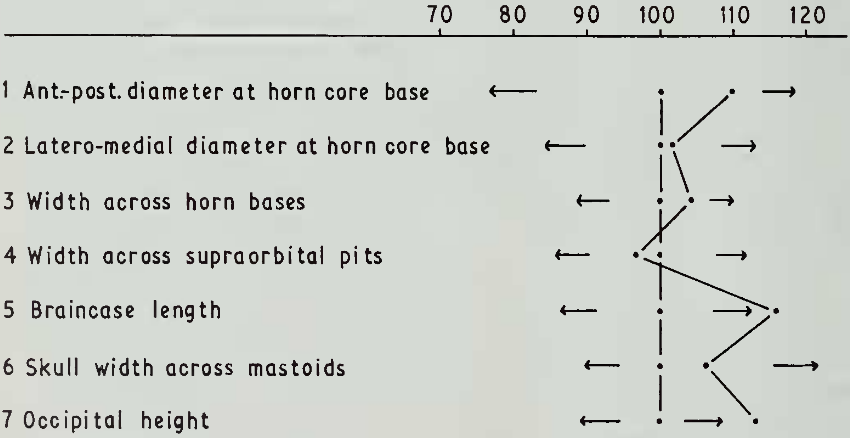

Fig. 6 Percentage diagram of skull measurements in elands. Braincase length is measured as in Fig. 5. The standard line at 100% is the mean of 12 living *Taurotragus oryx*, and standard deviations are also shown. The second line is for the holotype of *T. arkelli*, which has a longer and higher cranium, and supraorbital pits rather closer together than in *T. oryx*. The mediolateral compression of its horn cores may not differ much from large individuals of the living species.

no sinking of the braincase roof behind the horn cores to leave a narrow transverse crest across the top of the occipital. This last feature causes the angle of the parietal surface with the occipital to be more than 90° in the fossil, whereas it is less than 90° in the living species, as was noted by Leakey (1965 : 43). Other features seen on the cranium are typical of the living species: the long top edge of the occipital, the very poor median vertical ridge on the occipital with no flanking hollows, the long basioccipital and the large foramina ovalia. The size of the mastoid exposure is uncertain; it is certainly not larger on the occipital surface than in the living eland but the anterolateral edge is not clear. The horn cores of *T. arkelli* are short and not as divergent as in some individuals of extant west African and Sudanese populations called *T. oryx derbianus* and *T. o. gigas.* There is a weak posterior keel on the horn cores, and both the anterior and posterior keels are present to the tip of the left horn core.

Other remains of *Taurotragus* from Olduvai are part of a right horn core BM(NH) M 29415 from the surface of Bed II in 1935 and a small part of a left horn core M 29414 from Bed IV. In Nairobi there is a nearly complete left horn core with part of the frontal WK IV 1970.3641 and part of a right horn core 068/5924 which was a surface find at the Gorge and lacks the posterior keel. Species determinations are impossible for these pieces. The cranium E-58 and other remains from Olduvai of *T. oryx pachyceros* Schwarz (1937 : 33) which were originally in Munich were destroyed during the war. It is unfortunate that Schwarz did not figure the specimens; nothing in his descriptions suggests that they could have been from *T. arkelli,* and we shall abandon the use of his name.

MEASUREMENTS. Measurements on the cranium F.3665 P.P.T.4 of *Taurotragus arkelli* are:

Length of horn core along its front edge	430·0
Anteroposterior diameter of horn core at its base	71·5
Mediolateral diameter of horn core at its base	62·9
Minimum width across lateral surfaces of horn core pedicels	160·0
Width across lateral edges of supraorbital pits	85·9
Maximum braincase width	121·0
Skull width across mastoids immediately behind external auditory meati	179·0
Occipital height from top of foramen magnum to top of occipital crest	77·7
Width across posterior tuberosities of basioccipital	64·7

COMPARISONS. There are parts of two other fossil *Taurotragus* horn cores in the Nairobi collections, both lacking a posterior keel. They are the distal end of a right horn core from the Pleistocene deposits at Songhor, Kenya, and the basal part of a right horn core 068/6414 from Chemeron Plio-Pleistocene beds, found in 1966, which is larger than the horn cores of *T. arkelli.* The eland recorded by Hopwood (*in* Kent 1942 : 124) from Kagua, Kenya, on a right horn core base BM(NH) M 15874 is actually a kudu.

The piece of horn core in Berlin from Laetolil assigned to *Taurotragus* sp. cf. *gaudryi* (Thomas) by Dietrich (1950 : 43; pl. 4, fig. 46) is certainly of *Taurotragus* and from the right side but seems unlikely to be from the older fauna. For more remarks on *T. gaudryi* see p. 304. The right maxilla with P^4–M^3 which was also assigned to *Taurotragus* sp. cf. *gaudryi* by Dietrich (1950 : 43; pl. 3, fig. 41) has molars with rounded medial lobes and outbowed ribs between the styles, and is in fact bovine. It is probably conspecific with the teeth assigned to ? *Simatherium kohllarseni* (Dietrich 1950 : 44; figs 5, 32 and 36).

Arambourg (1947 : 434) referred to a large lower molar from the Shungura Formation, Omo, which he thought belonged to *Taurotragus*, and there is a mandibular fragment, P996-55, from member K as well as a molar fragment, Omo 28 68-2496, from member B, both of large size.

Eland fossils are fairly common at South African sites. A partial left maxilla BPI M.7 from Makapansgat Limeworks may be of a very large tragelaphine the size of *Taurotragus*; it was identified as *Taurotragus* cf. *oryx* by Wells & Cooke (1956 : 10). Cooke (1949 : 38, 44, 52) and Wells (1964b : 91) also listed *T.* cf. *oryx* from the Vaal River deposits, and Cooke & Wells (1951 : 205) recorded *T.* cf. *oryx* on teeth from Chelmer in Rhodesia.

Several crania and frontlets and many horn cores of *Taurotragus* occur at Elandsfontein. They are much closer to living *T. oryx* than to the Olduvai *T. arkelli* and the braincase tops are almost as short as in the living eland although the horn cores are perhaps more upright in their insertions. The Elandsfontein fossils would be younger than *T. arkelli* on the assumption that there has been but one lineage of *Taurotragus*. They illustrate very well the variability of the posterior keel on eland horn cores; it may be nearly absent, well-marked near the base, or well-marked from base to tip. It is better developed in males than females.

A piece of a juvenile right mandible and a large left lower molar from Florisbad may represent eland.

A frontlet with complete horn cores SAM Mb 70, a horn core fragment Mb 589 and parts of two mandibles Mb 10 and Mb 11 from Melkbos are of *Taurotragus oryx* (Hendey 1968 : 109). In Bloemfontein a cranium with complete horn cores C.2738 from Knoffelsvlei, Middelburg, and a frontlet with complete horn cores C.2797 from Mazelspoort are indistinguishable from the living eland.

Taurotragus oryx is common at Broken Hill, Zambia, as indicated by Leakey (*in* Clark 1959 : 229). The partial frontlet with left horn core BM(NH) M 12906 shows that it was more advanced than *T. arkelli.*

An eland is known from the later Pleistocene of north-west Africa, but disappeared at the start of the Holocene (Arambourg 1962 : 107). Arambourg (1938 : 42) referred to teeth from Ain Tit Mellil and El Khenzira in Morocco and figured a frontlet (pl. 9, fig. 3) from Casablanca. There is no evidence that these remains, nor a horn core from Pointe Pescade, Algeria (Pomel 1895 : pl. 7), are not the living species. Nothing in the illustrations or descriptions suggests they could be *T. arkelli.* However, the eland reported from the earlier site of Ternifine, Algeria (Arambourg 1962 : 106), is most unlikely to be of the living species.

Tribe **BOVINI**

This tribe comprises the late Tertiary to present-day descendants of different lineages of boselaphines. They are usually large and have low and wide skulls. The cranial features are: horn cores inserted at varying distances behind the orbits, without transverse ridges but sometimes with a very weak torsion, present in both sexes in living forms, frontals hollowed internally, the horn cores also internally hollowed in living species, preorbital fossae weak or absent, braincase shortened, infraorbital foramen tending to be low and anteriorly placed on the skull, basioccipital triangular in shape, molars with basal pillars and complicated central cavities, upper molars with prominent ribs between the styles, lower molars without large goat folds.

Among the living bovines, the cattle of Eurasia (*Bos* spp.) have wide frontals with horn core insertions set widely apart and so far back as to overhang the occipital, and have long faces. Bison of North America and Eurasia (*Bos bison* and *B. bonasus*) have wide skulls and short faces, and the short horn cores are inserted further forwards than in cattle but still behind the orbits. All species of *Bos* possess ethmoidal fissures, at least until the earlier part of adult life. Water buffaloes of southern Asia (*Bubalus arnee*) have long faces, very long and keeled horn cores inserted just behind the orbits, and a vomer fused to the back of the palate. There are also some smaller island forms of *Bubalus*. African buffaloes (*Syncerus caffer*) are short-faced and have horn cores inserted just behind the orbits. The horn cores are short and populations from east and southern Africa have enlarged basal bosses. The paraconid and metaconid on P_4 are generally fused. Among extinct genera, *Leptobos* Rütimeyer is clearly related to *Bos*, and *Proamphibos* Pilgrim and *Hemibos* Falconer to *Bubalus.*

In later Pleistocene deposits of Africa there are found large bovines generally similar to *Syncerus* but differing from it in their larger size, and in having long and less dorsoventrally compressed horn cores without basal bosses. Bate (1949) founded the genus *Homoioceras* for these buffaloes and (1951) recognized the following species:

Homoioceras singae Bate 1949, based on a skull with horn core bases from Singa on the Blue Nile, Sudan, and other fragments from the nearby site at Abu Hugar. This is the type species.

H. antiquus (Duvernoy 1851), from many sites in north-west Africa, mainly Algeria, well illustrated by Pomel (1893).

H. baini (Seeley 1891), from many sites in South Africa.

H. nilssoni (Lönnberg 1933), known only from a complete skull and skeleton from the River Melawa, near Naivasha, Kenya. The specimen is now in Stockholm. Its cheek teeth show considerable occlusal complexity.

It is important to reiterate Miss Bate's conclusion that these long-horned buffaloes resemble *Syncerus* and not *Bubalus*. They agree with *Syncerus* and differ from *Bubalus* in their shorter faces, keels not always present on the horn cores and frequently neither regular nor persistent, short nasals without lateral flanges anteriorly, premaxillae with only a short or no contact on the nasals, vomer not fused to the back of the palate, a lower and wider occipital, and a paraconid–metaconid fusion or approach to it on P_4. There are some limb bone similarities between *Syncerus caffer* and the skeleton of *Homoioceras nilssoni*, but it is not possible to ascertain differences from *Bubalus*, of which only one postcranial skeleton of *B. arnee* and one of the much smaller *B. depressicornis* are available in London. It is unfortunate that the holotype skull of *H. singae* most probably belongs to a short-horned buffalo, as was first suggested to us by J. W. Simons, and that the generic name *Homoioceras* is therefore a junior synonym of *Syncerus*.

A further large extinct African bovine is *Pelorovis oldowayensis* and its synonym *Bularchus arok*. The species was first described by Reck (1928) from Olduvai Gorge, and is not known outside East Africa. Reck had thought that his original cranium with horn cores belonged to a giant member of the Caprini, distantly related to sheep. However, one of the more striking later finds at Olduvai was a herd of *P. oldowayensis* at BK II in 1952 (Leakey 1954). It became clear from a study of this herd that *P. oldowayensis* is a bovine with an impressive number of resemblances to '*Homoioceras*' (Gentry 1967 : 287). The chief differences from '*Homoioceras*' are that the horn cores of *P. oldowayensis* are inserted close together and very posteriorly, passing backwards from their insertions then outwards, the face is longer, the tooth rows set more anteriorly and the occlusal pattern of the cheek teeth is simpler.

This assessment of *P. oldowayensis* was based on a comparison with the skeleton of '*H.*' *nilssoni*, the holotype cranium and Pomel's illustrations of '*H.*' *antiquus*, and a cast of the skull of *H. singae*. We have now seen much South African material of '*H.*' *baini*. The holotype in Cape Town is a cranium with horn cores, from alluvial deposits of unknown age of the Modder River, Orange Free State. There are also other remains from Cornelia, Florisbad and Vlakkraal in the National Museum, Bloemfontein. Those from Cornelia are an unnumbered face with tooth rows, a left maxilla C.918, a right mandible C.918 and a right M_3 C.2857; those from Florisbad are a right maxilla C.1476, part of a left mandible C.2902, and two unnumbered left and right upper molars, and from Vlakkraal there is a cranium C.1538 with long horn cores without basal bosses. Finally, Cooke & Wells (1951 : 205, fig. 1) described an upper tooth row from Chelmer, Rhodesia. The occlusal pattern of the molars of '*H.*' *antiquus* and the Cornelia and Chelmer '*H.*' *baini* is slightly less complicated than in '*H.*' *nilssoni*. The Florisbad animal is slightly smaller and has similar teeth and a mandible which is not very deep below M_3.

The Elandsfontein material in the South African Museum, Cape Town, may be the best existing collection of long-horned buffaloes. Many of the cheek teeth, especially those in earlier wear, have markedly simple occlusal surfaces. This is manifested in small basal pillars, a simple outline of the central cavities, little outbowing of the ribs between the styles on the upper molars and a less 'pinched in' appearance of the lateral lobes of the lower molars. In later wear they appear to be as advanced as at other sites, but not to match the complexity seen in '*H.*' *nilssoni*. Furthermore, the premolar row is unusually long, and there is practically never any paraconid–metaconid fusion on P_4, whereas in other '*Homoioceras*' this occurs in later wear. There are few other differences except perhaps flatter nasals, a less deep zygomatic bar below the orbit and narrower anterior tuberosities of the basioccipital. The somewhat simplified occlusal morphology of the cheek teeth in the Elandsfontein buffalo weakens the generic difference between '*Homoioceras*' and *Pelorovis*. It thus seems best to place all the extinct long-horned bovines of Africa in one genus *Pelorovis*. There are two species, *P. oldowayensis* for the animal first described from Olduvai, and *P. antiquus* for the other fossils. Further, more detailed work may show the trivial names *baini* and *nilssoni* to have continuing usefulness at subspecies level. Our supposition is that *P. antiquus* is closer to *P. oldowayensis* than to short-horned buffaloes of the *Syncerus* lineage, and may be the descendant of *P. oldowayensis*.

Genus *PELOROVIS* Reck 1928

1928 *Pelorovis* Reck : 57.
1936 *Bularchus* Hopwood : 639.

TYPE SPECIES. *Pelorovis oldowayensis* Reck 1928.

GENERIC DIAGNOSIS. Extinct large African bovines with massive, long, curved horn cores, slightly compressed dorsoventrally and without keels; both sexes with horns; frontals hollowed internally; no ethmoidal fissures; no preorbital fossae; premaxillae either not reaching the nasals or having only a short contact; nasals fairly short; vomer not fused to the back of the palate; occipital low and wide; P_4s with paraconid and metaconid growing close together and usually fusing in late wear.

HORIZON. From the Shungura Formation, Omo, surviving until the end of the Pleistocene.

REMARKS. *Homoioceras* is not placed as a synonym because the type species is based on a *Syncerus* specimen (p. 309). However, *Pelorovis* includes all other species formerly referred to *Homoioceras*.

Pelorovis oldowayensis Reck 1928

1928 *Pelorovis oldowayensis* Reck : 57, text-fig. 1; pls 1 and 2.
1936 *Bularchus arok* Hopwood : 639, no figure.

DIAGNOSIS. Horn cores not hollowed internally, inserted close together and so far posteriorly as frequently to overhang the occipital surface, curved backwards from the base, then outwards and finally forwards and a little upwards; nasals domed transversely; anterior part of the zygomatic arch thickened below the orbits; anterior tuberosities of the basioccipital rather wide apart for a bovine; molars with small basal pillars and central cavities simple in outline; upper molars with poorly localized and outbowed ribs between the lateral styles; mandibles with deep horizontal rami.

HOLOTYPE. A cranium with horn cores in Berlin, field numbers 1516, 1517 and 1518.

HORIZON. The holotype was found on the north side of the Gorge near the human burial at the site now known as RK. Dietrich (1933 : 299) wrote that it came from Bed IV. The species is plentiful at Olduvai, but the other remains are all from middle and upper Bed II except for a mandible and a tooth from Bed III. The species is also known from Kanjera and probably from the Shungura Formation, Omo.

REMARKS. Gentry (1967) listed material from SHK II and BK II at Olduvai, including two complete skulls from the latter site. Material from other sites was less plentiful, and consisted of a left mandibular fragment and a distal metatarsal from MRC II, a right astragalus 1959.211 from KK II, a distal metacarpal 1957.367 from the surface of FC II and a seventh cervical vertebra from an unknown level at HWK II. Teeth have subsequently been found at MNK II and in the highest levels of HWK East II (Pl. 11, fig. 1). Part of a left mandible BM(NH) M 29460 comes from Bed III and was probably found in 1931 ('III' is written on it with the yellow ink used on several 1931 fossils); P_3–M_3 are present in early wear but with extensively cracked enamel walls, and have quite a simple occlusal pattern which fits *P. oldowayensis*. On P_4 the metaconid is growing towards the paraconid, but fusion has not yet occurred at this early stage of wear. A right upper molar, JK III/4, 1969.607, also fits *P. oldowayensis*.

Gentry (1967 : 290) discussed the hypodigm of *Bularchus arok* Hopwood, and decided that it was the same species as *Pelorovis oldowayensis*. The holotype frontlet, BM(NH) M 14947, probably came from PLK at the top of Bed II (M. D. Leakey, personal communication and 1971b : 283). Gentry (1967 : 291; pl. 5, figs 3 and 4; pl. 6) also discussed the second complete skull found with the BK II herd in 1952. Compared with the first, probably female, skull, it had longer horn cores which were more compressed, inserted less posteriorly and not overhanging the occipital, the zygomatic arch deeper anteriorly, the tooth row positioned less anteriorly (Fig. 7, readings 5 and 6), the occipital surface lower and wider, the anterior tuberosities of the basioccipital wider and the mandibular ramus slightly shallower. It seems better to accept this skull as lying within the

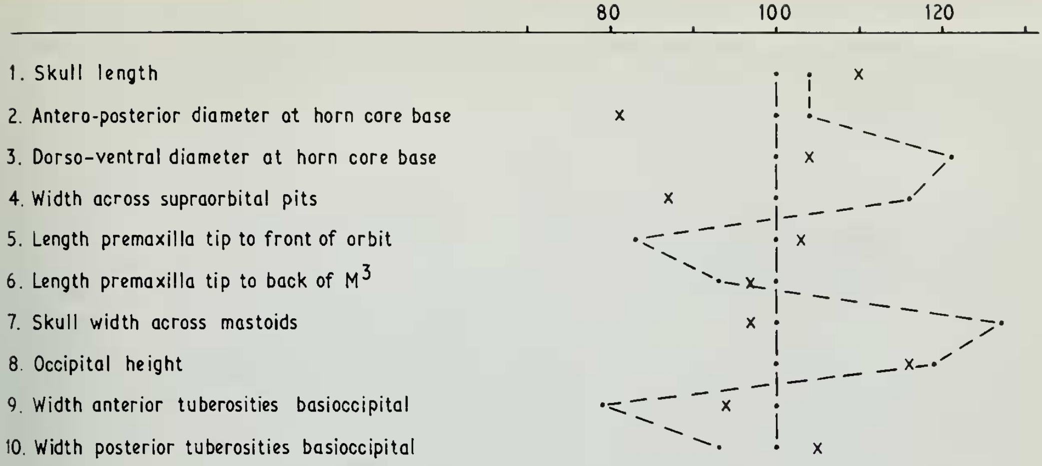

Fig. 7 Percentage diagram of skull measurements in Bovini. The standard line is for the BK II skull of *Pelorovis oldowayensis* which is probably a male; the second line is for the *P. antiquus* skull from Naivasha, Kenya. Crosses mark the readings for the supposed female skull of *P. oldowayensis*. The male *P. oldowayensis* has strong compression of its horn cores; *P. antiquus* has larger horn cores, a shorter face (readings 5 and 6), a very wide and relatively low occipital and narrow anterior tuberosities on the basioccipital.

range of variation of *P. oldowayensis* than to place it in a separate species, particularly as it was found in the same herd as the first skull. In many of its characters it shows signs of approach to *P. antiquus*, as in those of the horn cores, the position of the tooth row, the shallower mandible and the proportions of the occipital.

COMPARISONS. *Pelorovis oldowayensis* is known from Kanjera by a pair of mandibles BM(NH) M 15856 (referred to *Bularchus arok* by Hopwood *in* Kent 1942 : 126), a left upper molar M 25676, part of a left upper molar M 25688, part of a right upper molar M 25677, an incomplete left M_3 M 25692 and three tooth fragments M 25679–81 (Gentry 1967 : 291). There are also many horn core pieces.

Pieces of large curved horn cores from members D, F, and G of the Shungura Formation, Omo, may well belong to *Pelorovis*, if not to *P. oldowayensis*. They include L.16-(9 + 81) and L.16-101. A few bovine teeth from members C, E and F are large enough for assignment to *Pelorovis*, but are not morphologically distinguishable from *Syncerus*. This situation is a contrast to that with the bovine teeth of middle and upper Bed II at Olduvai.

The cranium of *Simatherium kohllarseni* Dietrich (1941 : 221; 1942 : 119; pl. 20, figs 161, 163 and 165) from the Vogel River, Laetolil, numbered Vo 670 in Berlin, is almost as large as *Pelorovis oldowayensis* and could be its ancestor. The horn cores are long, dorsoventrally compressed, strongly divergent, inserted obliquely in side view, and large in relation to skull size, all of which are resemblances to *P. oldowayensis*. There are three interesting differences: the horn cores are inserted less far backwards (well forwards of the level of the occipital surface), the insertions are wider apart, and the end of the left horn core, as preserved, is beginning to curve more backwards and less outwards. The first and last characters can reasonably be expected in an ancestral form; in fact it is noteworthy that the lessening divergence of the distal parts of the horn cores in *Simatherium* is closer to other primitive bovines such as *Proamphibos* and *Leptobos* than is *Pelorovis*. Dietrich himself linked the Laetolil cranium with *Parabos* Arambourg & Piveteau. The wide insertion of the horn cores in *Simatherium* is less obviously a primitive character, but we consider it is not suffiicient to remove the species from a possible ancestry to *Pelorovis*. Dietrich (1950 : 44; pl. 1, fig. 5; pl. 3, figs 32 and 36) assigned to ? *Simatherium kohllarseni* some teeth which do not differ from other early bovine teeth. To become *P. oldowayensis* they would have to increase in size without acquiring a more complex occlusal pattern.

Two horn core fragments from Langebaanweg, L.4615 and L.6586, may represent *Simatherium* or an allied genus. They are large and curved and L.4615 has a very prominent keel. This caused Gentry (*in* Hendey 1970a : 114) to identify the horn cores wrongly as kudus. Some of the bovine teeth at Langebaanweg are notably large.

Pelorovis antiquus (Duvernoy 1851)

1851 *Bubalus antiquus* Duvernoy : 597, no figure.
1891 *Bubalus baini* Seeley : 201, figure.
1933 *Bubalus nilssoni* Lönnberg : 28; pls 1–3.

DIAGNOSIS. A species of *Pelorovis* with horn cores normally curved fowards and downwards from the base, inserted widely apart and behind the orbits but less posteriorly than in *P. oldowayensis*; anterior part of the zygomatic arch not thickened below the orbits; face shorter and tooth row set less anteriorly than in *P. oldowayensis*; occipital surface low and wide; molars with larger basal pillars and central cavities more complicated in outline, and upper molars with more localized and outbowed ribs between the styles than in *P. oldowayensis*.

HOLOTYPE. A cranium with horn cores in the Institut de Paléontologie, Paris.

HORIZON. The holotype came from near Setif in the Department of Constantine, Algeria. Thomas (1881 : 119) named the site as Oued Bou Sellam, and Romer (1928 : 88, 109) quoted an opinion of Joleaud that it came from between the 30 and 15 metre terraces, and hence might be of Lower Monastirian (between Tensiftian and Soltanian) age, which would be an equivalent of the early part of the last glaciation. However, the 15 and 30 metre terraces, at least in Morocco, could lie within the time span from the Holstein to the early Eem interglacials (Butzer 1972 : 24). Thus the holotype may come from the Upper or Middle Pleistocene.

Thomas (1884 : 17–18; pl. 4, fig. 6) attributed to this species a horn core tip from deposits of Villafranchian-equivalent age at Mansoura, but we do not believe that one can be certain of the species identification for such a fragment. It is difficult to find convincing north African occurrences of *P. antiquus* before the Middle and Upper Pleistocene, and Pomel (1888 : 229) remarked in connection with a possible Lower Pleistocene record at Palikao (=Ternifine), Algeria, that it is more especially characteristic of later sites. We can be sure that this species nearly always occurs later than *P. oldowayensis*. At Olduvai Gorge it is known from upper Bed IV.

REMARKS. The species is represented at Olduvai by the greater part of a right horn core WK East IV 1970 A.2305 (5) (Pl. 4, fig. 1). When complete this horn core would not have been so long as some other specimens from other parts of Africa. It is compressed dorsoventrally, without clear keels or transverse ridges, is inserted immediately behind the orbit so that its front edge is level with the supraorbital pits, emerges transversely in dorsal view and only very slightly upwards in front view, and curves gently backwards. There is a very small supraorbital pit and no sign of a temporal ridge behind the horn base. The length along the front curve as preserved is *c*. 790 mm, the anteroposterior basal diameter 134 mm and the dorsoventral diameter *c*. 80 mm.

It is possible that *P. antiquus* descends from *P. oldowayensis*. The different course of the horn cores ensures a more stable distribution of their weight on either side of the skull and may be linked with the usual but not invariable decline in anterior thickening of the zygomatic arch in *P. antiquus*. (The East African individual called *nilssoni* still has a thickened arch.) Increasing the massiveness of horn cores with a backwards then outwards curvature would lead to mechanical problems which could be ameliorated by such a change in course. Perhaps the second complete skull of *P. oldowayensis* in the BK II herd shows the first signs of this with its insertions being less posterior. The low level of the horn core tips on this skull (Gentry 1967 : pl. 5, fig. 3) could have been an increasing impediment to eating and drinking, and hence another reason for an evolutionary change. The same individual also shows other characters like *P. antiquus* (p. 310). A less likely alternative is that *P. antiquus* descended from some mid-Pleistocene *Syncerus* like that of Olduvai Bed II. *P. antiquus* agrees with this *Syncerus* in the general course of the horn cores, the shape of their basal cross-section and the clear temporal ridges at the side of the braincase roof.

If *P. antiquus* did descend from *P. oldowayensis*, the transition seems likely to have occurred during the time span of Olduvai Bed IV according to the evidence of a *P. antiquus* horn core in upper Bed IV and the supposed provenance of the *P. oldowayensis* holotype in Bed IV. The transition need not have taken place in East Africa, and it is still not known that the improved teeth evolved synchronously with the horn core changes. A *P. oldowayensis* mandible BM(NH) M 29460 is known as late as Bed III, as has already been noted. Other bovine dentitions and individual teeth from Bed III as a whole are not quite as large as the teeth of *P. oldowayensis*, but have larger basal pillars, more marked indentations into the central cavities and perhaps stronger and more localized ribs on the lateral walls of the upper molars. It is best to leave them as *Syncerus* for the present, and to suppose that tooth size increased in that lineage between Bed II and Bed III. However, changes in the stratigraphical interpretation of Olduvai Gorge need affect only a few fossil pieces in order to upset this evolutionary picture.

COMPARISONS. Part of a large left mandible from Peninj is possibly *P. antiquus*. This is A67.282 (WN64.256.MPI) probably from the Moinik Formation overlying the Humbu Formation (Isaac *in litt.*). The localized outbowings of the medial walls and constricted lateral lobes of the molars are more advanced than in *P. oldowayensis*. The occlusal length of M_2 is 35·1, and of M_3 49·8 mm. Dietrich (1950 : 47, fig. 56) described what are evidently fragments of a *P. antiquus* skull from the 'young Pleistocene' of the Eyasi area, Tanzania.

P. antiquus is present at Broken Hill, Zambia, as was noted by Leakey (*in* Clark 1959 : 229). The material registered as BM(NH) M 12143 includes parts of more than one *P. antiquus* skull, as well as a piece of a rhinoceros. Leakey noted how much this material differed from the holotype of *Homoioceras singae* but did not question the latter's identity as a long-horned buffalo.

Bate (*in* McBurney & Hey 1955 : 282, fig. 39) recorded *Homoioceras* sp. on two horn core bases from the late Pleistocene of Wadi Derna, Libya. One of the horn cores is registered BM(NH) M 16619. A skull from Bizerta, Tunisia could be *P. antiquus* (Bate 1951 : 19) but has horn cores passing directly outwards from their bases instead of slightly forwards (Solignac 1924 : pl. 6, fig. 1). The horn core base from Kom Ombo, Sudan, of '*Bubalus*' *vignardi* Gaillard (1934 : 37; pl. 5, figs 1–2) was noted by Bate (*in* Arkell 1949 : 24; 1951 : 18) as not resembling any other buffalo. A cast of it in London, M 16688, looks like *Bos primigenius*. Churcher & Smith (1972 : 260) and Churcher (1972 : 62) found *Bos primigenius* at Kom Ombo but no definite *Pelorovis antiquus*.

Genus *SYNCERUS* Hodgson 1847

TYPE SPECIES. *Syncerus caffer* (Sparrman 1779).

GENERIC DIAGNOSIS. Moderate-sized to large African bovines with wide skulls and short faces; horn cores short to moderately long, dorsoventrally compressed, often with keels, and emerging transversely from just behind the orbits; females with horns; supraorbital pits fairly close together; occipital surface low and wide; molars with moderate-sized basal pillars and central cavities without such an extremely complicated outline as in *Bos*; upper molars without such pronounced ribs between the styles as in *Bos*; the occlusal complexity of the teeth increasing with increased body size; P_4 with paraconid and metaconid growing towards one another or fused.

The following characters, known only from the living species, are quite likely to be valid for the genus: nasals fairly short, without lateral flanges anteriorly, and in a plane nearly parallel to the tooth row giving the face quite a high profile; no ethmoidal fissures; no preorbital fossae; premaxillae with only a short or no contact on the nasals; vomer not fused to the back of the palate.

REMARKS. The genus contains two species, the type species *Syncerus caffer* and a new fossil species from Olduvai. In the following account of the Olduvai species we have received much assistance from J. W. Simons.

Syncerus acoelotus sp. nov.

DIAGNOSIS. A *Syncerus* in which the horn cores emerge transversely, curve gradually backwards with a slight twist which is anticlockwise on the right side, but do not pass very markedly or at all ventrally in their basal parts, are internally hollowed only near their bases and as an extension of the hollowing of the frontals, are triangular in cross-section with an anterior, upper and lower surfaces, and with almost a keeled edge between the upper and anterior surfaces, and are only slightly compressed dorsoventrally. Frontals with a rugose surface in some individuals but horn cores lacking large basal bosses; anterior tuberosities of the basioccipital probably wider apart than in *S. caffer*; P_4s with paraconid and metaconid not fused but growing closer to one another.

Holotype. A cranium with both horn cores 068/5811 recovered in 1962 (Pl. 2). It is at present in the National Museum of Kenya, Nairobi.

Horizon. The holotype came from basal gravels at Kar K, upper Bed II, Olduvai. Some other specimens with horn cores range from middle Bed II to undivided III–IV, and teeth occur from Beds I to IV.

Remarks. The specific name refers to the absence of internal sinuses above the base of the horn cores, and is taken from the Greek κοῖλος (coelos), 'hollowed'. In the holotype the lateral parts of the occipital surface are missing, the right orbital rim is imperfect and only the dorsal surface of the left is preserved. The surface of the frontals is somewhat rugose between the horn core bases, and the frontals are only a little updomed, insufficiently so for there to be an associated concavity of the nasion. The cross-section of the horn cores is subtriangular becoming more oval towards the tips. The anterior surface of the horn cores is flattened proximally but becomes gradually more convex nearer the tips. Distally the horn cores curve very slightly downwards. From the massiveness of the horn cores and the rugosity of the frontals, the holotype seems to be a male. An atlas and axis vertebrae and probably also a third cervical are associated with this cranium.

Other crania of *Syncerus acoelotus* are now in Dar es Salaam. OF 67.48 was collected from FK West upper Bed II in 1962. It is probably a male although the horn cores are less massive at their bases and longer than in the holotype. The right horn core is complete to the tip and the partly reconstructed left is almost entire. The horn cores tend to have a flat top surface and an anterior keel in their lower parts; their basal cross-section approaches a triangular shape more than in the holotype. They emerge transversely, then curve backwards and slightly upwards, the backward component of the curvature being accentuated towards the tips. The right horn core is internally hollowed at about 120 mm above the base, but only in its posterodorsal part; there are no sinuses at about 250 mm short of the tips on either side. The frontals have a smooth top surface and extensive sinuses. They are slightly more convex longitudinally than in the holotype. The occipital surface is definitely wide, but less extremely so than in *Pelorovis antiquus*. The auditory bulla appears to have been somewhat compressed.

OF 68.274 is a juvenile collected from the surface of site Bos K III–IV in 1962. It is a skull with horn core bases and tooth rows, but without the back or base of the braincase. The horn core bases show no signs of keels; they have a more oval cross-section and are inserted with a more backward component than in adults. The right supraorbital foramen alone is preserved, and it is slightly larger than in adults. At the back of the palate the median indentation does not reach quite as far anteriorly as the two lateral ones. The vomer is almost certainly not fused with the back of the palate. Part of the left horn core of this specimen is detached from the skull and is numbered OF 68.205.

OF 68.196 collected in 1961 at VFK high in Bed III–IV, and almost certainly of Bed IV age, is labelled 'XDK IV'. It is poorly mineralized and consists of frontals with horn core bases. The occipital and ventral surface of the skull are completely absent. The frontals are flat and lack any surface rugosity, and the horn cores are hollowed as far as preserved. The horn core bases are more pear-shaped, with an approach to a posterior keel, and less triangular in cross-section than in other specimens. There is no clear anterodorsal keel. Possibly this specimen is from a female.

A much weathered frontlet of a small *S. acoelotus* was found in 1973 in Elephant Korongo in conglomerate 1·5 m above the Lemuta Member (Pl. 4, fig. 2). The horn cores are shorter and squatter than in previous examples. There is some dorsoventral compression of the horn cores, a more or less flat dorsal surface proximally, an anterodorsal keel proximally, and a slight

Plate 2 (Scale = 100 mm)

Syncerus acoelotus holotype. Dorsal and ventral views of cranium with horn cores, Kar K II 1962.068/5811.

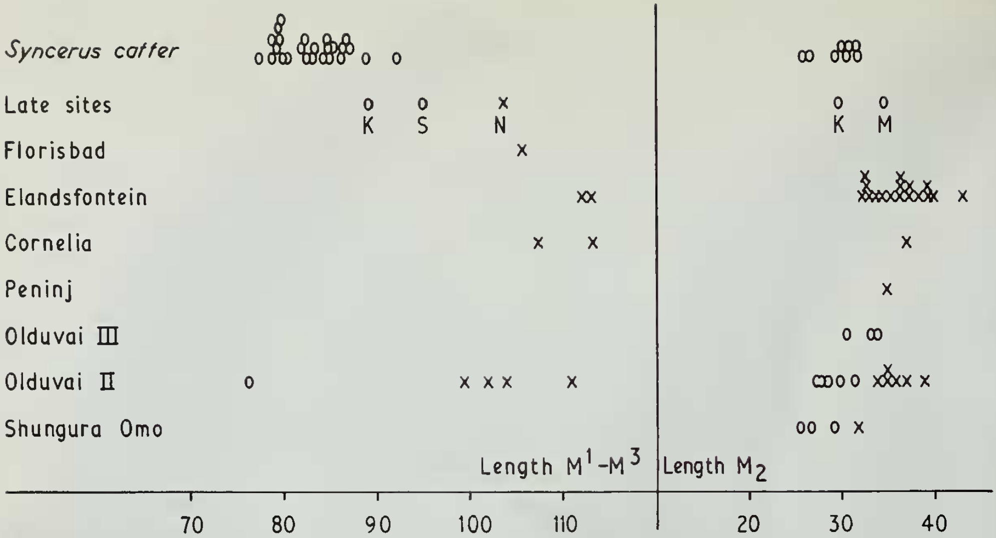

Fig. 8 Tooth measurements in Bovini. O = *Syncerus* lineage, X = *Pelorovis* lineage. K = Kibish Formation buffalo, N = Naivasha *P. antiquus*, M = Melkbos buffalo, S = '*Homoioceras*' *singae* holotype.

demarcation of a ventral and an anteroventral surface, the former being largely constituted by a posteroventral shallow concavity in the basal half of the horn core. The horn cores arise immediately behind the orbits with very wide divergence and pass slightly upwards with a gentle backward curvature. The frontals are updomed by reference to the parietal surface posteriorly, but not nearly so much as in living *S. caffer caffer*. They have a rugose surface between the horn core bases as in the holotype, and an internal system of sinuses. The top of the braincase is not very angled on the face axis, and the right temporal ridge is preserved and is as sharply demarcated as in the holotype. The chief interest of this specimen is whether the short horn cores were typical of the whole species at this early time, or whether they indicate only a forest or woodland race, comparable with *S. c. nanus* at the present day.

Bovine teeth found in Bed III, principally at the JK2 sites, seem more likely to belong to *S. acoelotus* than to *Pelorovis antiquus*, as has been mentioned already (p. 313). In Bed II some of the bovine teeth found at BK II differ from *P. oldowayensis* by being smaller (Fig. 8) and often with a more complicated occlusal morphology. They too must be *S. acoelotus*, although smaller than the Bed III teeth. In the three P_4s on BK mandibles 1953.067/5230 (Fig. 9; Pl. 1, fig. 4), 1963.2717 and 1963.2765 there is no fusion of paraconid with metaconid to form a complete medial wall at the front of the tooth, and this differs from living *S. caffer* and from *P. oldowayensis*. However, the metaconid is growing towards the paraconid, and perhaps fusion would have taken place in later wear. In the mandible 1953.067/5230 the ratio of premolar to molar row length

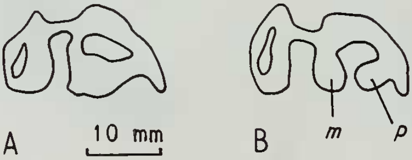

Fig. 9 Occlusal pattern of bovine left P_4s. The anterior side is towards the right of the page. A = extant *Syncerus caffer*, B = *S. acoelotus* BK II 1953.067/5230. *m* = metaconid, *p* = paraconid.

would have been greater than in most *S. caffer*, but not beyond the range for that species. A right maxilla, Rhino K 068/6655 (Pl. 3) probably from upper Bed II, has rather a large M^2 but the occlusal morphology matches *S. acoelotus*. Part of a right mandible 068/5795 may have been associated with the cranium from FK West II.

Similar bovine teeth occur at sites DK I, FLK I, FLKN I, HWK East II levels 1 and 2, and TK II. At FLKN I the teeth are perhaps less advanced than those of Bed II in occlusal complexity. It is likely that all these teeth come from a single *Syncerus* lineage, but we do not know how far back it may be called *Syncerus acoelotus*.

The fragment of right mandible with P_3 and P_4 said by Dietrich (1937 : 109; pl. 6, fig. 6) to be from STK II and described as *Bubalus* sp. was most probably of this lineage. Fusion of paraconid to metaconid on P_4 has not taken place.

Some limb bones from Olduvai are likely to be bovines of this lineage, and include a left humerus from FK West II. Others will be mentioned in the accounts of the sites, in Part II.

Survival of *Syncerus* into Bed IV at Olduvai is indicated by a bovine left M_3 and a left lower molar WK East IV A.1922 (3) and A.1698 (3), both found in 1970 and both too small for *Pelorovis*. The occlusal length of the M_3 is 45·3 mm. These teeth are counted in Tables 11 and 12 as *Syncerus acoelotus*.

The Olduvai fossils differ from the Asian water buffalo *Bubalus arnee* in that the front of the horn cores is closer to the back of the orbits, the triangularity of the horn core cross-section is less distinct since the anterodorsal edge between the top and the front surface of the horn cores is less marked and set at a less anterior level, the orbital rims project less, there is a tendency to an irregular bony growth over the surface of the frontals between the horn core bases which seems to foreshadow boss formation, and the supraorbital pits are set closer together. The distance between the supraorbital pits expressed as a percentage of skull width across the back of the orbits was 49 in the holotype of *Syncerus acoelotus*, whereas in eight skulls of *B. arnee* it had a range of 55–62, with a mean value of 58 (Gentry 1967 : 271). These characters all take the fossils closer to

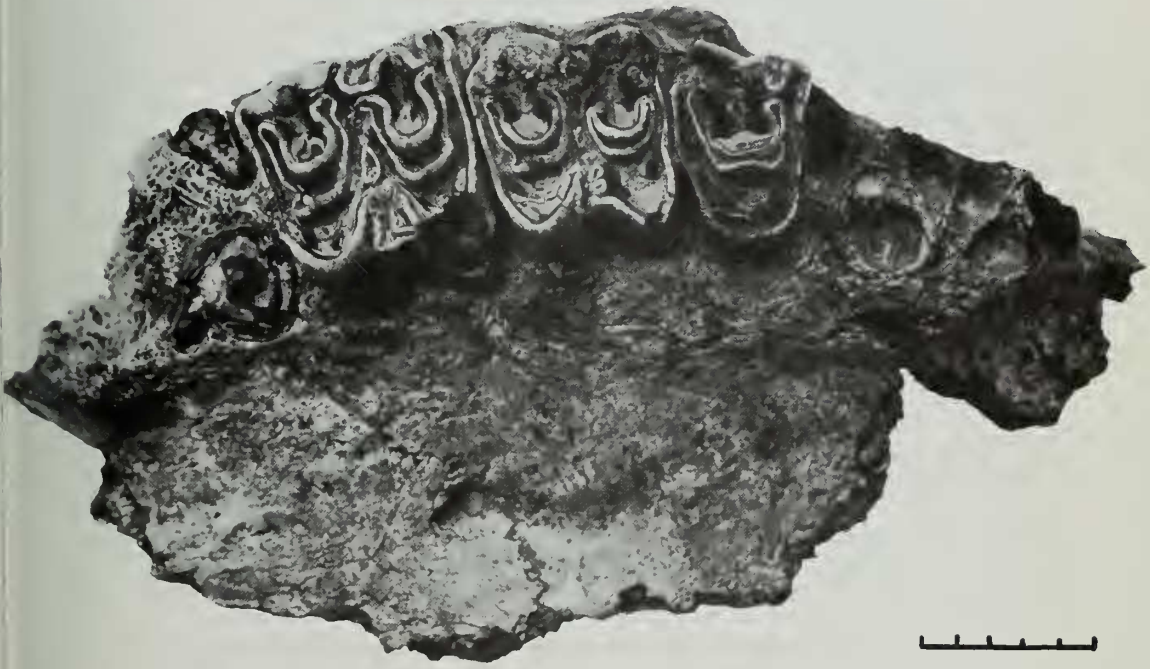

Plate 3 (Scale = 25 mm)

Syncerus acoelotus. Right maxilla with P^4–M^2, Rhino K II surface 1962.068/6655.

Syncerus caffer, and we can be sure that *S. acoelotus* does not represent an Asian element in the Olduvai fauna. On the contrary, it appears to be very close to the living African buffalo.

Grubb (1972) accepts a minimum of four subspecies within the living *Syncerus caffer*. *S. c. nanus* comprises small forest forms with short horns inserted widely apart, curving outwards and backwards from the base, and lying more or less in the facial plane. There is frequently an anterodorsal keel on the horn cores between the dorsal surface and what almost amounts to an anterior surface. *S. c. brachyceros* embraces the west African savannah buffaloes ranging as far east as the River Chari. They intergrade clinally along their boundary with *S. c. nanus*, and are larger, the males having more divergent horns, dipping slightly from the facial plane and with bases approaching closer to the midline of the skull. *S. c. aequinoctialis* intergrades secondarily with *S. c. brachyceros* in the Chari region and ranges further east into the Sudan. It is a still larger savannah buffalo with larger horns which dip ventrally. *S. c. caffer* embraces the eastern and southern savannah or Cape buffaloes. The males are characterized by greatly enlarged horn bases approaching very closely to one another across the top of the swollen frontals, and horn cores dipping considerably downwards and showing so much dorsoventral compression that hardly anything of an anterior surface remains at all. Buffaloes of either of the last two subspecies intergrade secondarily with forest buffaloes along the western or Albertine Rift Valley.

There is no doubt that the Olduvai buffalo agrees most nearly with buffaloes of the first two subspecies despite their smaller size. If a forest buffalo were to grow larger without acquiring the horn specializations of the Cape buffalo, it would much resemble *S. acoelotus*. Valid differences of *S. acoelotus* from *S. caffer* remain as the less extensive hollowing of the horn cores, less dorsoventral flattening of the horn core, less complete fusion of paraconid with metaconid on P_4 and wider anterior tuberosities of the basioccipital. One can see it as ancestral to *S. caffer*, and the present-day Cape buffaloes as a very late specialization in which the great growth of the basal bosses is linked with downturning and dorsoventral flattening. Perhaps we are witnessing the origin of a new species for which the evolutionary opportunity may have been the recent disappearance of *Pelorovis antiquus*.

MEASUREMENTS. Measurements on the cranium 068/5811 from Kar II are:

Length of horn core along its front edge	c. 650·0
Anteroposterior diameter of horn core at its base	137·0
Mediolateral diameter of horn core at its base	110·0
Minimum width across lateral surfaces of horn core pedicels	256·0
Width across lateral edges of supraorbital pits	125·0
Occipital height from top of foramen magnum to top of occipital crest	76·0
Width across posterior tuberosities of basioccipital	72·6

Measurements on the cranium OF 67.48 from FK West II are:

Length of left horn core along anterodorsal keel	680·0
Length of right horn core along anterodorsal keel	800·0
Occipital height from top of foramen magnum to top of occipital crest	77·5
Width across posterior tuberosities of basioccipital	72·8

Measurements on the cranium OF 68.196 from VFK III–IV are:

Anteroposterior diameter of horn core at its base	c. 109·0
Mediolateral diameter of horn core at its base	c. 73·0
Width across lateral edges of supraorbital pits	135·0

Measurements on the immature cranium OF 68/274 from the surface of Bos K III–IV are:

Occlusal length deciduous P^2 to deciduous P^4	c. 68·0
Occlusal length M^2	c. 32·0

Measurements on the frontlet S.271 from Elephant Korongo, middle Bed II are:

Length of horn core along its front edge	370·0
Anteroposterior diameter of horn core at its base	103·0
Mediolateral diameter of horn core at its base	82·6

The maxilla BK II 1963.2757 had occlusal lengths M^1–M^3 and M^2 of 76·3 and 27·1 mm, and the maxilla Rhino K 068/6655 had M^2 at 31·4 mm.

Measurements on mandibles likely to be *Syncerus acoelotus* are:

	BK II 1953.067/5230	BK II 1963.2717	BK II 1963.2765	JK2 GP8 III GN 24
Occlusal length M_1–M_3	91·4	–	–	101·1
Occlusal length M_2	28·7	–	29·9	30·8
Occlusal length P_2–P_4	*c.* 56·0	56·8	*c.* 58·0	–

Occlusal lengths of M_2 on four mandibles are:

FK West II 068/5795	28·0	BK II 1963.2818	27·9
BK II 1953.067/5229	31·5	JK2 III A.2833	33·3

Measurements of length and least thickness of two limb bones of *S. acoelotus* are:

Metatarsal	SC II 1962.068/6662	228 × 31·3	Metacarpal	BK II 1952.218	217 × 38·1

COMPARISONS. *S. acoelotus* is distinguished from '*Homoioceras*' *singae* Bate of the Sudan (see p. 309) by the triangular cross-section, little dorsoventral compression, better-marked anterodorsal keel of the horn cores and wider anterior tuberosities of the basioccipital. '*H.*' *singae* can probably be regarded as a large race of *Syncerus caffer* in which the basal bosses and downward sweep of the horn cores of *S. c. caffer* are lacking. It has sinuses extending into its horn cores to at least 140 mm above the dorsal base, and probably they would have extended still further in those parts of the horn core which are not preserved.

A skull and nearly complete skeleton of a large *Syncerus caffer* were found by the 1967 Kenya contingent of the Omo Research Expedition at site KS in the same horizon of the Kibish Formation as a human skeleton (R. E. F. Leakey 1969 : 1132). The skull differs from *S. c. caffer* in the lack of any pronounced uparching of the frontals connected with basal boss formation on its horn cores, in the lack of surface rugosity of the frontals and in the horn cores not passing appreciably downwards after their emergence from the frontals. The skull resembles the less advanced west African and Ethiopian buffaloes more than *S. c. caffer*, yet it is the size of a rather large male of the latter subspecies. It differs from *S. acoelotus* in the horn cores becoming very dorsoventrally compressed immediately above the base, and in the tips being more strongly curved upwards. The limb bones are larger than half a dozen examples of living *S. c. caffer*. The metasarsals are missing, but the metacarpal may be relatively slightly longer. Morphologically the limb bones resemble *Syncerus* in the valley between the articular head and great trochanter of the femur, the short medial malleolus at the distal end of the tibia (by reference to the tibia's central anterior flange and not to the back of the medial side of the bone, which is broken), and the absence of a rim on the medial side of the proximal medial facet of the radius.

Some skull fragments from the Shungura Formation including some horn cores from member C represent a small and very short-horned *Syncerus*. The horn cores, e.g. L.744-1, L.837-2 and Omo 18 sup 1967.153, have a strong concavity on the posteroventral surface near their base, and thus resemble the Olduvai frontlet from Elephant Korongo more closely than any other *S. acoelotus*. Some surface rugosity appears on the frontals between the horn bases. Like the Olduvai *Syncerus*, they are dorsoventrally compressed, with a flat dorsal surface, emerge sideways and slightly upwards from the skull and have sinuses in their frontals. As discussed above in connection with the Elephant Korongo frontlet, the shortness of these horn cores suggests either the primitive condition for the lineage or a forest-inhabiting race. The backs of two bovine crania, L.2-26 from member B and L.607-1 from member G, are probably conspecific and have a less shortened braincase than in *S. caffer*. Their occipital surfaces are as low and wide as in Cape buffaloes and relatively lower and wider than in the smaller forest buffaloes. Bovine teeth from the Shungura Formation, very like those of Olduvai Bed I, are also likely to belong to the *Syncerus* lineage.

The *Syncerus* lineage is represented at Kanjera by the back part of a left upper molar BM(NH)

M 25715, a tooth smaller and with a more complicated occlusal pattern than *Pelorovis oldowayensis* at the same site. Other Kanjera teeth of the same species are left upper molar M 25683, right lower molar M 25697, left lower molar M 25705 and left P_4 M 25678.

Bovine teeth are found in both the later and the earlier faunas of the Kaiso Formation (Cooke & Coryndon 1970 : 201, 202; the teeth M 12595a and M 12601 assigned by them to *Hippotragus* sp. are also bovine).

A large buffalo at Melkbos (Hendey 1968 : 104) is represented by a partial cranium with horn core bases, other horn cores, dentitions and limb bones. The horn cores are internally hollowed, and the extremely marked surface rugosity of the frontals extends over the entire area between the horn core bases and the mid-dorsal line of the skull. Both these characters are advanced over the condition of *S. acoelotus*, and must align the Melkbos fossils with *S. caffer*. However, they differ from living East and southern African Cape buffaloes, *S. c. caffer*, in that the horn cores pass only outwards and do not turn downwards immediately above their bases. The whole frontal area itself is flat and not domed.

At Elandsfontein the only bovine fossils not assignable to *Pelorovis* are a right lower molar SAM 20526 and a right metacarpal 20814. Their size and proportions fit *Syncerus caffer*.

A *Syncerus* is represented by a right lower tooth row from P_4 to M_3 BM(NH) M 25304, and probably by parts of an immature right and left lower dentition M 25303, from the Chiwondo Beds at Mwenirondo, Malawi. These were recorded as hippotragine by Coryndon (1966 : 66).

Bubalus andersoni Scott (1907 : 256; pl. 16, figs 4 and 4a) is a large lower jaw from the Zululand coast on which only M_2 and M_3 remain, their respective occlusal lengths being given as 32 and 45 mm. This is perhaps a large fossil *Syncerus*.

At Makapansgat Limeworks two upper molars BPI M.31 and M.32 are perhaps bovine. The occlusal complexity of these teeth is not very advanced but they are not as large as in *Pelorovis oldowayensis* as known from Bed II Olduvai and Kanjera. Their basal pillars are rather small, the styles not very pronounced, the central cavities simple in outline and the outbowings of the lateral walls between the styles not very localized or pronounced. The right mandible BPI M.15 and immature left mandible M.10 referred to 'cf. *Syncerus caffer*' by Wells & Cooke (1956 : 11) have ribs on the lateral surface of the upper molars and medial surface of the lower molars better marked than in the above. Given that regional and temporal size variations might, and did, occur in either of the bovine lineages, it is difficult to know how to place the Makapansgat specimens. It is perhaps best to regard M.31 and M.32 as connected with *P. oldowayensis*, either as a rather small variety or as representing an earlier time level of the lineage than Bed II at Olduvai, and M.10 and M.15 as connected with *Syncerus*.

One of the most interesting bovines to be found in Africa is the holotype skull, BM(NH) M 25307, of *Ugandax gautieri* Cooke & Coryndon (1970 : 206; pls 17 and 18) from Kaiso Formation deposits of unknown age in the Kazinga Channel, Uganda. Although published as a hippotragine, the skull has many similarities to *Proamphibos* Pilgrim from the Tatrot Formation of the Siwaliks. Compared with BM(NH) M 26576, a plaster cast of the holotype skull of the type species *Proamphibos lachrymans* Pilgrim (1939 : 271; pl. 5, figs 3–6), *U. gautieri* agrees in its fairly large size, very little compression of the horn cores, the degree of divergence of the horn cores, their course, their inclination in side view, their fairly wide insertions with little projection of the orbital rims, no raising of the frontals between the horn core bases, a marked anteriorly-directed central indentation of the parietofrontal suture, strong temporal ridges, the degree of bending down of the braincase on the facial axis, the short braincase, small supraorbital pits, strong nuchal crests and the triangular shape of the basioccipital. The horn core on the *U. gautieri* skull does not have the strong anterior keel nor the posterolateral keel of *P. lachrymans*, but its cross-section shows the same basic shape (Fig. 10).

Ugandax gautieri has some differences from the Indian species. These are its shorter horn cores, the less orderly surface pattern of ridges and grooves at the horn core base, the insertions less far behind the orbits, lack of a preorbital fossa, a wider and less high occipital surface, the anterior tuberosities of the basioccipital further apart, a central longitudinal ridge on the basioccipital, the basisphenoid apparently rising at a less marked angle on the plane of the basioccipital, smaller basal pillars on the upper molars, and styles less pronounced and ribs less localized on the lateral walls of the upper molars. Some of these features are more primitive than in *P. lachrymans*, notably the shorter horn cores, anteroposterior level of the horn insertions, the angle of the basisphenoid, and the tooth characters, but the different surface texture at the base of the horn cores, absence of a preorbital fossa and low occipital surface suggest that *U. gautieri* is better regarded as a separate African stock which has retained some characters in a more primitive condition than *P. lachrymans*.

1

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Plate 4 (Scales = 100 mm)

Fig. 1 ***Pelorovis antiquus***. Dorsal view of right horn core, WK East IV 1970.A.2305 (5).

Fig. 2 ***Syncerus acoelotus***. Dorsal view of frontlet, Elephant K II above the Lemuta Member.

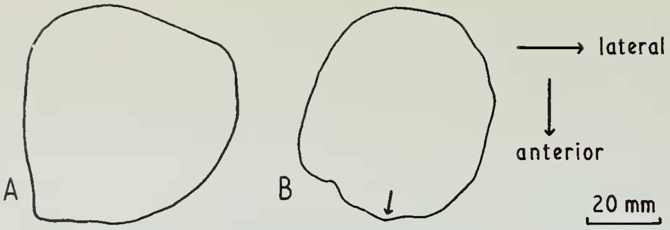

Fig. 10 Cross-sections near base of horn cores.
A = *Proamphibos lachrymans*, cast of holotype; a cross-section of the right horn core has been reversed to appear as of the left side. B = *Ugandax gautieri* holotype, left horn core. The most important of the irregular partial keels of *U. gautieri* descends at the position marked by the arrow.

Pilgrim (1939 : 276) took the reasonable view that *Proamphibos* gave rise through *Hemibos* to the living Asiatic water buffaloes *Bubalus*. If the Kazinga Channel deposits were sufficiently old, *Ugandax gautieri* could be near the start of the lineage of the African buffalo *Syncerus*. The near-absence of keels on its horn cores, less neat surface texture at the base of the horn cores, lower occipital surface, wider basioccipital anterior tuberosities and perhaps the less advanced teeth are all compatible with this view. *U. gautieri* is too primitive a species for us to expect any more definite indications of relationship. One possible intermediate between *U. gautieri* and *Syncerus acoelotus* is the Shungura Formation *Syncerus*, already mentioned above. This has an occipital surface still lower and wider than in *U. gautieri* and probably a shorter braincase, and such a trend in development of skull proportions parallels what took place in the evolution of *Bubalus*. The *Simatherium–Pelorovis* lineage is also related to the *Syncerus* lineage, and might also have come from a form like *U. gautieri*. Perhaps the three bovine successions, *Leptobos* to *Bos*, *Proamphibos* to *Bubalus* via *Hemibos*, and *Ugandax* to *Syncerus*, all arose from a genus such as *Pachyportax* Pilgrim in the upper Miocene. In view of the past connections of Indian and African bovid faunas (Gentry 1970a : 316–317) it is interesting that *U. gautieri* agrees so well with the Siwaliks *Proamphibos*. However, a careful study of the European Pliocene fossils of *Parabos* Arambourg & Piveteau might demonstrate equally close resemblances of *Ugandax* to this European bovine.

Tribe **CEPHALOPHINI**

Schwarz (1937 : 25) referred a mandible and some vertebrae from Olduvai to *Philantomba monticola* subsp. This species, the living blue duiker, is the smallest of the duikers and is now usually included in *Cephalophus*. Schwarz gave no illustrations and his material was lost in the Second World War. We have excluded this species from the Olduvai list.

Tribe **REDUNCINI**

The tribe contains two living genera, *Redunca* H. Smith, the reedbucks, and *Kobus* A. Smith, the kob, lechwes and waterbuck. Reduncines are moderate-sized to large grazing antelopes, and as indicated by their vernacular names, are commonly found in habitats near water (Lamprey 1963 : 69, fig. 7; Hirst 1975 : 32). Their characteristic skull features are: horn cores inserted above the orbits, without keels of any length or spiralling but with transverse ridges, frequently set obliquely in side view and concave anteriorly from the base up, postcornual fossae present, females without horns. Frontals with very little development of internal sinuses, frontals not rising to a higher level between the horn core bases than the top of the orbital rims, midfrontal and parietofrontal sutures fairly complicated, temporal ridges of the braincase roof often approaching closely to one another, living forms without preorbital fossae, ethmoidal fissures large, lateral flanges absent anteriorly on nasals, maxillary tuberosity prominent in ventral view, infraorbital foramen tending to be low and anteriorly-placed on the skull, basioccipital with large anterior tuberosities, foramina ovalia moderate to large, palatal ridges on the maxillae in front of the tooth rows coming close together. Teeth moderately hypsodont, rather small in relation to skull and mandible size, upper and lower molars with basal pillars, medial lobes of upper molars and lateral lobes of lower molars constricted, upper molars with small but protruding ribs between the styles, lower molars with goat folds, upper and lower P2s small, lower premolars with an appearance of antero-posterior compression, P_4s with a strongly projecting hypoconid and often a deep and narrow lateral valley in front of it, P_4s usually without paraconid–metaconid fusion to form a complete medial wall anteriorly.

Redunca redunca (Pallas 1777), the bohor reedbuck, occurs from Senegal eastwards to Ethiopia and as far south as Tanzania. It has short horns (except *R. redunca cottoni* in the southern Sudan) with tips recurved forwards. It lives in areas with long grass near water.

Redunca arundinum (Boddaert 1785), the southern reedbuck, is found from Tanzania southwards and has long and divergent horns, less thickened at the base than in *R. redunca*. About half the P_4s show close approach or even fusion of paraconid and metaconid.

Redunca fulvorufula (Afzelius 1815), the mountain reedbuck, has a discontinuous distribution in southern Africa, some parts of eastern Africa, and in northern Cameroun. It has short and little divergent horns, less thickened at the base than in *R. redunca*. The orbits are larger than in the other two species. It lives on rocky sloping grassland with light cover, which is an unusual habitat for a reduncine.

Kobus kob (Erxleben 1777), the kob, including *K. vardoni* (Livingstone 1857), the puku, occurs from south-western Kenya and Uganda westwards to Senegal and as far south as Botswana. The horn cores show some mediolateral compression, curve backwards at the base, and are inserted close together in anterior view and uprightly in side view. Gentry (1970a : 282) has commented that the limb bones are more cursorially adapted than in other reduncines. It favours grasslands close to water, frequently the higher parts of floodplains.

Kobus leche Gray 1850, the central African lechwe, has horn cores which are mediolaterally compressed, inserted wide apart and obliquely at the base, and curved backwards at the base. The species is markedly gregarious on the lowest-lying parts of floodplains.

Kobus ellipsiprymnus (Ogilby 1833), the waterbuck, is the largest living reduncine. It occurs from Somalia westwards to Senegal and as far south as Natal. The horn cores are little mediolaterally compressed, inserted wide apart and obliquely at the base, and are curved upwards from the base and eventually forwards. The species lives in savannah country with access to water and browses more frequently than *K. kob* or *K. leche*.

Kobus megaceros (Fitzinger 1855), the Nile or Mrs Gray's lechwe, occurs in marshy areas of reeds or tall grass around the papyrus 'sudd' swamps in the southern Sudan, and in the Gambella region of Ethiopia (Blower 1967). It has a very distinctive skull morphology. The horn cores are inserted further behind the orbits than in other reduncines, the braincase is short and angled on the facial axis, the nasals are wide and the longitudinal ridges on the basioccipital are very strong.

Among fossil reduncines *Kobus sigmoidalis* Arambourg is a likely ancestor for waterbuck and the central African lechwe. Fossil kobs are also known, but no distinct species have been named. Early *Kobus* seem likely to have had horn cores inserted obliquely and close together. The kob stock retained the oblique insertions for a time and showed less mediolateral compression of the horn cores than in *K. sigmoidalis*. By the time of Olduvai Bed III kobs had acquired more uprightly-inserted and more compressed horn cores, while the waterbuck line had developed less upright and less compressed horn cores. The skull became lower and wider in the latter group, rather as in *Redunca*. The living kob has acquired or retained a braincase more angled on the facial axis than in *Redunca* or other *Kobus*; it also has a noticeably smoothly-rounded edge of the occipital surface which is like some *Redunca*. Two or more reduncines from the Pinjor and Tatrot Formations of the Siwaliks are congeneric or close parallels to *Kobus*.

Redunca probably derived from smaller forms with wider skulls and more upright horn cores than *Kobus*. The only undoubted fossil species is *R. darti* Wells & Cooke. *R. ancystrocera* Arambourg may be linked with the very large and unique Olduvai fossil named *Thaleroceros radiciformis*, and is better classified as belonging to *Kobus*. A final group of reduncines, unrepresented at Olduvai, is constituted by the Omo, Kaiso and Marsabit Road (2°30′ N, 37°27′ E) form *Menelikia lyrocera* Arambourg 1941.

Genus ***KOBUS*** A. Smith 1840

TYPE SPECIES. *Kobus ellipsiprymnus* (Ogilby 1833).

GENERIC DIAGNOSIS. Larger-sized reduncines; horn cores usually long, their bases sometimes curving backwards instead of being concave anteriorly, with a flattened lateral surface but no tendency towards a flattened posteromedial surface; frontals sometimes with a small system of internal sinuses.

REMARKS. Generic level definitions are difficult and unsatisfactory in the Reduncini because of the differences within *Kobus* between kobs and the waterbuck–central African lechwe group, the uncertain generic placing of some fossils, the independent appearance of characters in different lineages, and because of some instances of opposing directions of character evolution in different lineages. Living *Kobus* species are more gregarious than reedbucks, but a behavioural trait is not useful for the interpretation of fossils.

Kobus sigmoidalis Arambourg 1941

1941 *Kobus sigmoidalis* Arambourg : 346, fig. 5.
1947 *Kobus sigmoidalis* Arambourg : 411; pl. 27, fig. 4; pl. 28, fig. 3.
1947 *Kobus* (*Kobus*) sp. Arambourg : 415, text-fig. 61.

DIAGNOSIS. An extinct species of *Kobus* about the size of the living waterbuck or central African lechwe; horn cores long, mediolaterally compressed, without keels, with transverse ridges, more divergent basally than in waterbuck then with lessening divergence distally, and with a weakly sigmoid curvature at the base so that they curve first backwards then upwards. Temporal ridges approaching quite closely posteriorly, top edge of occipital fairly evenly rounded, median occipital ridge with a flanking fairly flat surface, mastoids often with a strong ventral rim and often without a marked depression around the mastoid foramen, basioccipital with large anterior tuberosities, auditory bullae inflated and moderate-sized. Upper molars retaining the primitive characters of central cavities that are often not very complicated and ribs between the styles that are not very localized or accentuated; lower molars probably with less constricted lateral lobes more frequently than in the living waterbuck.

HOLOTYPE. A cranium, 145, found in the Omo beds in 1932–33 and now in Paris.

HORIZON. The horizon of the holotype is unknown. In the Shungura Formation the species is present in members C and D and common in E, F and G. At Olduvai it is quite common in Bed I; it occurs at Kaiso and it, or a descendant, at Kanjera.

REMARKS. *Kobus sigmoidalis* is best known from Omo. The Olduvai material is larger and includes an incomplete right horn core (Pl. 5, figs 1, 2), part of the same skull with basioccipital and auditory bullae, and nearly complete maxillae, all numbered FLKNN I 1961.871. The right side of a crushed, immature skull with horn core base 296 also came from FLKNN I. A frontlet with the basal halves of both horn cores 068/6506, and associated palate 068/6502, was found in 1961 in gravel postdating the Ndutu Beds and probably of Holocene age near the base of the Gorge at FLKNN I; from the type of fossilization and the adherent calcareous incrustation it probably originated in Bed I or lower II and was redeposited (M. D. Leakey, personal communication). The basal part of a left horn core BM(NH) M 14542 found in 1932 and the basal part of a right horn core with the midfrontal suture and supraorbital pit M 29419 both came from Bed I.

K. sigmoidalis is too large to be connected with living *Redunca* and is unlike a kob or Nile lechwe, so it is necessary to differentiate it from the waterbuck and central African lechwe. The

Plate 5 (Scale = 50 mm for the horn core and 25 mm for the dentitions)

Kobus sigmoidalis

Fig. 1 Lateral view of right horn core, FLKNN I 871.

Fig. 2 Anterior view of same horn core.

Fig. 3 Occlusal view of left P^2–M^3, FLKNN I 535.

Fig. 4 Occlusal view of right P_3–M_3, FLK I G.388.

differences from the waterbuck comprise the characters mentioned in the diagnosis with the reservation that not all available individuals of the living species, or even a majority of them, have more advanced upper molars. The living waterbuck is larger, its horn cores are less compressed (Fig. 11), less divergent and often shorter, beginning to rise from their bases instead of from their middle sections, the temporal ridges are wider apart, the occipital surface has pronounced hollows on either side of its median vertical ridge and its edge is not smoothly rounded, the mastoids are larger, without a pronounced ventral rim and frequently with a small deep depression around the mastoid foramen.

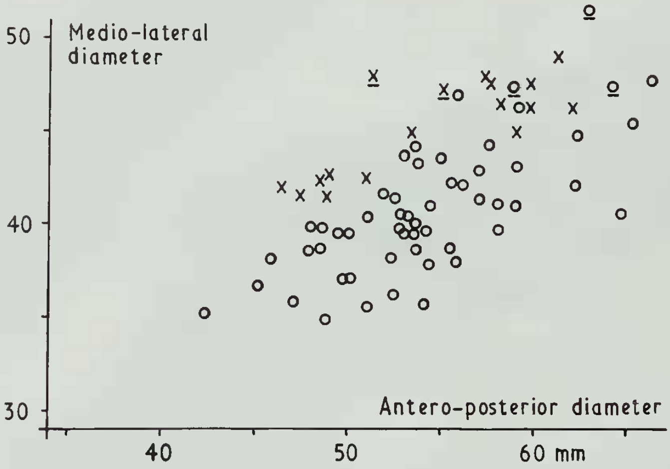

Fig. 11 Basal horn core dimensions of some reduncines.

O = *Kobus sigmoidalis* from member G of the Shungura Formation, X = *K. ellipsiprymnus*, O̲ = Olduvai *K. sigmoidalis*, X̲ = Olduvai *K. ellipsiprymnus*. *K. sigmoidalis* is larger at Olduvai than at Omo.

In all these characters *K. sigmoidalis* resembles the lechwe *K. leche*, but we prefer to regard it as no more closely related to this species than to *K. ellipsiprymnus*. Our opinion arises from the teeth of Olduvai *K. sigmoidalis* being much larger than those of *K. leche* and from the horn core evidence of a transition from *K. sigmoidalis* to *K. ellipsiprymnus*. Good *K. sigmoidalis* occurs as high as member G of the Shungura Formation and early in Olduvai Bed I. A minority of Shungura member G horn cores, e.g. L.25-15 and L.518-8, are intermediate between *K. sigmoidalis* and *ellipsiprymnus* in the degree of basal backward curvature and mediolateral compression. Probably the transition to *K. ellipsiprymnus* occurred within the time span of Olduvai. Horn cores from Beds I?, III and the III–IV junction, and some Shungura pieces, e.g. F.203-27 from member K and the middle part of a horn core F.164-25 from member G, are more definitely like waterbuck. *K. leche* is perhaps also a descendant of *K. sigmoidalis*, showing less alteration in its morphology but a specialized way of life.

A hornless female skull of a large *Kobus* S.202 (Pl. 6) was found in Bed I in 1970. It came from geologic locality 63. It is almost complete and lacks only the left P^4, right premaxilla, top of the left premaxilla, front of the nasals and part of the zygomatic arch. Some distortion has occurred. It is smaller than adult females of the living waterbuck, the back half of the braincase probably descends rather steeply, and the basioccipital has a markedly deep central longitudinal groove. The identification of this specimen as *K. sigmoidalis* or *ellipsiprymnus* is difficult: the temporal ridges approach one another closely, the mastoid is slightly narrower than in the waterbuck and lacks a pronounced ventral rim, and the median occipital ridge and flanking hollows are slightly better marked than in some Omo male *K. sigmoidalis*. We will take this suite of characters as supporting assignment to *K. sigmoidalis*, but it does not seem very decisive particularly if one reflects that early *K. ellipsiprymnus* would not be so distinct from *K. sigmoidalis* as is present-day *ellipsiprymnus*.

The considerable number of reduncine dentitions from Olduvai Bed I, including many immature ones, agree in size and morphology with those associated with the horn core 871 and frontlet 068/6506, and on the female skull S.202. They are presumably all of *K. sigmoidalis* or perhaps early *K. ellipsiprymnus*. The adult tooth rows are about the size of those of living waterbuck, but

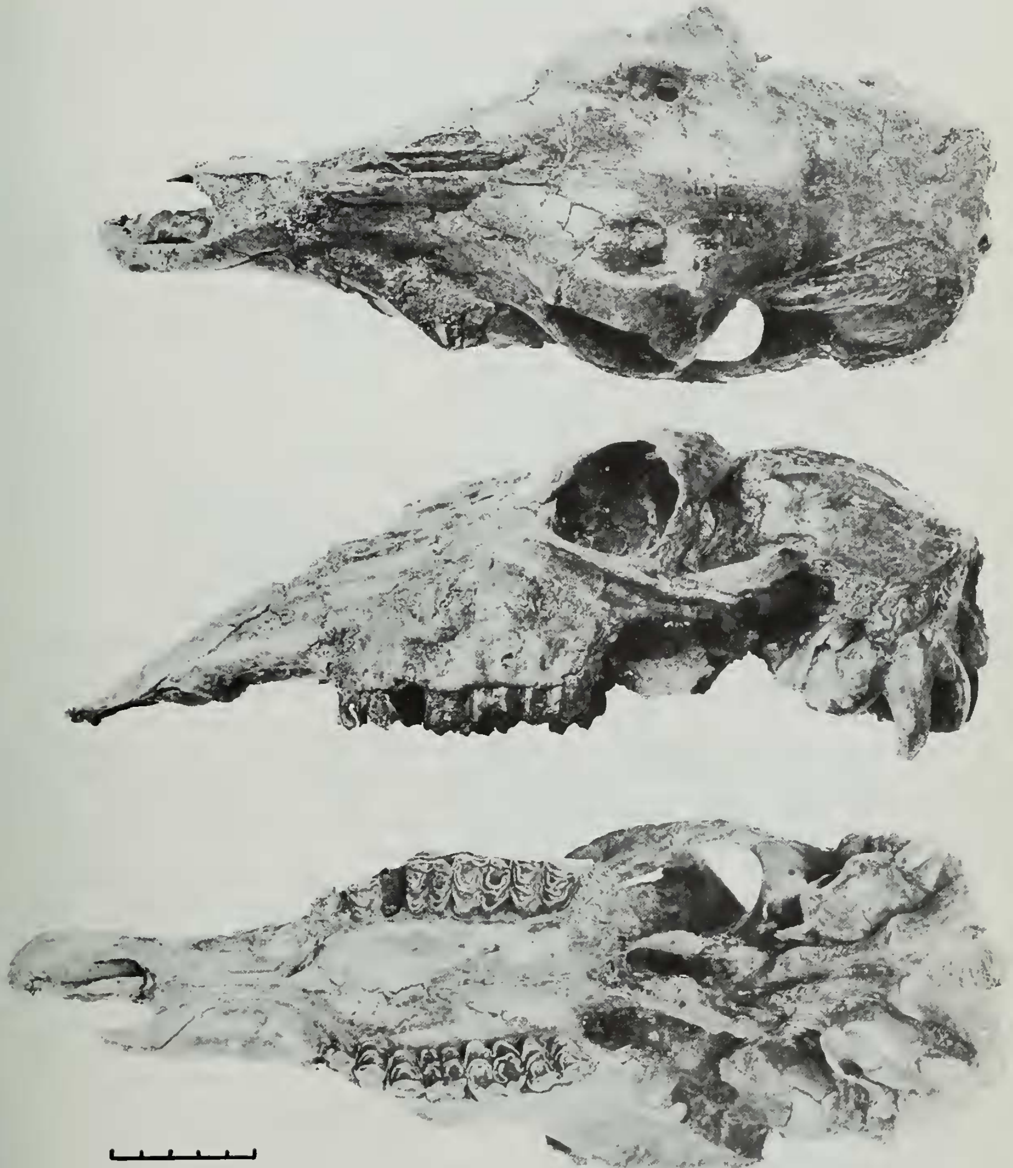

Plate 6 (Scale = 50 mm)

Kobus sigmoidalis. Female skull S.202 from Bed I in dorsal, lateral and palatal views.

four measurable specimens (maxilla FLKNN I 535, skull S.202 and mandibles FLKNN I 64 and FLK I D.41) suggest that the premolar row could be shorter. Both mandibles have premolar row lengths at the lower end of the distribution for Recent *K. ellipsiprymnus* (Fig. 12). As already mentioned, *K. sigmoidalis* molars have a rather unprogressive morphology, and this is true of specimens in a middle stage of wear which is the period when any evolving complexity would be most easily detectable. Large samples of teeth from the living species and from successive horizons at Olduvai and other sites could be expected to demonstrate the gradual appearance of, for example, localized and accentuated ribs on the lateral walls of the upper molars. Reduncine teeth of a size appropriate for *K. sigmoidalis/ellipsiprymnus* continue to occur in lower Bed II, and there is a single occurrence from middle Bed II just above the Lemuta Tuff Member. This is a left M_3 HWK EE II 1123 with an occlusal length of 30·2 mm.

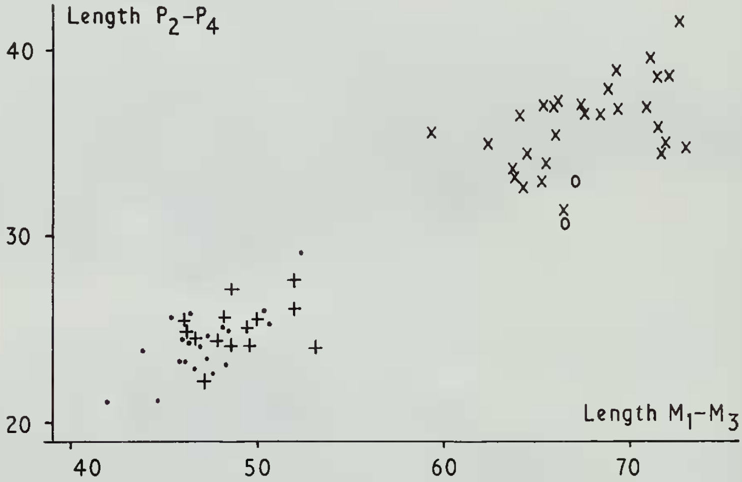

Fig. 12 Premolar/molar row proportions for some reduncines.
X = living *Kobus ellipsiprymnus*, + = living *K. leche*, ● = living *K. kob*, O = right mandibles FLK I 1960.D41 (above) and FLKNN I 1960.64 (below).

The Bed I reduncine limb bones are also probably of *K. sigmoidalis*. Fig. 13 (p. 332) shows that the long metapodials and rather long radius have proportions nearer to lechwe than to waterbuck. Further details are given in the account of the FLKNN I site in Part II.

MEASUREMENTS. Measurements on *K. sigmoidalis* are:

	FLKNN I 871	FLKNN I 068/6506 +068/6502	Bed I M 29419
Anteroposterior diameter of horn core at its base	64·3	59·0	63·1
Mediolateral diameter of horn core at its base	47·6	47·3	51·5
Occlusal length M^1–M^3	–	67·8	–
Occlusal length M^2	21·0	*c.* 23·7	–

Measurements on the female skull S.202 are:

Skull length from front of the premaxillae to back of the occipital condyles	332·0
Skull width across posterior side of orbits	131·0
Width across lateral edges of supraorbital pits	67·6
Length from back of frontals to top of occiput	77·8
Maximum braincase width	84·9
Skull width across mastoids immediately behind external auditory meati	100·5
Distance from rearmost point of occlusal surface of M^3 to back of occipital condyles	140·0

Occipital height from top of foramen magnum to top of occipital crest	45·4
Occlusal length M^1–M^3	57·1
Occlusal length M^2	19·6
Occlusal length P^2–P^4	34·2

Measurements on two maxillae assigned to *K. sigmoidalis* are:

	FLKNN I 535	FLK I B.46
Occlusal length M^1–M^3	63·1	–
Occlusal length M^2	22·8	21·5
Occlusal length P^2–P^4	40·2	–

Measurements on the more complete mandibles assigned to *K. sigmoidalis* are:

	FLKNN I					FLK I	
	13	64	131	920	965	D.41	G.388
Occlusal length M_1–M_3	–	66·6	–	63·5	77·8	67·1	68·0
Occlusal length M_2	–	20·2	20·1	20·4	23·2	20·8	20·2
Occlusal length P_2–P_4	35·1	30·7	35·2	–	–	33·0	–

Measurements on the M_2s of 10 mandibles from FLKNN I and FLK I, including those from the mandibles whose measurements are listed above, are:

	Number measured	Mean	Range	Standard deviation	Standard error
Occlusal length M_2	10	21·1	20·1–23·2	1·1	0·35

Measurements of length and least thickness on some associated sets of limb bones assigned to *K. sigmoidalis* are:

FLKNN I	radius 370	244 × 34·2,	metacarpal 369	230 × 28·0
FLKNN I	radius 890	250 × 29·2,	metacarpal 889	228 × 24·1
FLKNN I	radius 499	249 × 37·5,	metacarpal 498	238 × 28·7
FLK I	radius C.1094	259 × –,	metacarpal C.1095	241 × –
	humerus C.1092	270 × 31·7		

Measurements of length and least thickness of other limb bones assigned to *K. sigmoidalis* are:

DK I	radius 788	236 × 34·5
FLKNN I	metacarpal 616	205 × 20·3
FLKNN I	metatarsal 738	225 × 25·3

COMPARISONS. The base of a right horn core from Kanjera, BM(NH) M 25633, is either *K. sigmoidalis* or *K. ellipsiprymnus* on account of its degree of mediolateral compression and absence of backwardly-directed curvature at the base.

An unregistered left horn core in London, labelled 'KAISO I', much resembles *K. sigmoidalis*. This may be the piece collected by Bishop at Nyawiega which Cooke & Coryndon (1970 : 214) referred to *Pultiphagonides* cf. *africanus*. It is interesting that Nyawiega fossils are thought to come from the earlier Kaiso faunal assemblage, perhaps as old as 4–5 million years, which would make the Nyawiega horn core older than the *K. sigmoidalis* of the Shungura Formation, Omo.

A cranium L.2604 and some short horn cores from Langebaanweg may be a *Kobus* species (Gentry *in* Hendey 1970a : 115). The oblique horn core insertions and very upright pedicels, and the closeness of the insertions, could all be primitive in *Kobus*. A flattened lateral surface and some degree of mediolateral compression are like *K. sigmoidalis*. The species is unlikely to belong to *Redunca* since it is larger than the Makapansgat Limeworks fossil *R. darti*, has more oblique and closely inserted horn cores, a higher occipital surface without an evenly rounded edge, large auditory bullae, larger anterior tuberosities of the basioccipital and larger mastoids without a ventral rim. The best solution seems that the Langebaanweg remains represent a short-horned relative or ancestor of *K. sigmoidalis*.

One of the reduncine crania from the Pinjor Formation of the Siwaliks and now in London has some resemblance to *Kobus sigmoidalis*. This is BM(NH) 39559a, referred to as *Vishnucobus patulicornis* (Lydekker) by Pilgrim (1939 : 102). It is a little smaller than *Kobus sigmoidalis*, and agrees in having fairly divergent horn cores. It is unlike the East African species in its larger supraorbital pits situated close together, and more primitive in its prominent temporal ridges and less compressed horn cores inserted more closely together. If the Pinjor Formation were earlier than the later levels of the Shungura Formation at Omo, it is possible that 39559a might be the actual ancestor of *K. sigmoidalis*. Further discussion of Siwaliks reduncines will be found under kob on p. 337.

The type cranium of *Kobus venterae* Broom (1913 : 13) from Florisbad, SAM 2323, differs from *K. leche* only in the slightly more upright horn core insertion in side view, but the doubtful precision with which the horn core has been affixed makes this uncertain. The skull is low and wide and lechwe-sized. The horn cores would have been inserted wide apart in anterior view and above the back of the orbits. The surviving right horn core is very compressed with a flattened lateral surface and lacks keels or transverse ridges. It has a slightly convex front edge in profile at the base as in *K. sigmoidalis*. The upper part of the median occipital ridge is preserved and shows shallow hollows on either side. The mastoid exposure is moderately-sized. There is no clear sign of a ventral rim to the mastoid, nor of the small depressed area cut dorsomedially quite deeply into the occipital, frequently found in the waterbuck. The anterior tuberosities of the basioccipital are not as large as in the waterbuck and resemble the lechwe. The cranium is best regarded as belonging to *K. leche*. Similar horn cores in Bloemfontein from late Pleistocene sites are probably the same species. Several specimens come from Florisbad, including an unnumbered frontlet and left and right horn cores both numbered C.1458, which are larger than the holotype, two left mandibles, C.1473 and one without number, and a left lower molar. Other horn cores come from Mahemspan (C.1940), Mockesdam (C.2679), Vlakkraal (four numbered C.1541) and Cornelia (Cooke 1974 : 77). These remains give valuable information for palaeoecological analysis, because of the close association of *K. leche* with seasonally inundated flood plains.

Kobus ellipsiprymnus (Ogilby 1833)

DIAGNOSIS. A large reduncine species; horn cores moderately long with some mediolateral compression, little or moderate divergence, transverse ridges generally well marked, without any backward curvature at the base but rising with their concave edge anteriorly; temporal ridges of the cranial roof may approach closely or remain more widely apart; top edge of occipital not evenly rounded, median ridge on the occipital flanked by small depressions near its top; mastoids not narrow, without a strong ventral rim but with a marked depression around the mastoid foramen, and tending to face laterally in males. P_4s in late wear may show fusion of paraconid and metaconid.

REMARKS. Some Olduvai horn cores are likely to be of waterbuck, as previously mentioned in the discussion of *K. sigmoidalis*. These are a left horn core with the frontal suture, supraorbital pit and orbital rim 068/6658 from the surface of EF-HR III–IV junction in 1962 (Pl. 7, fig. 2), the basal part of a left horn core JK2 GP8 III 1654 found in 1961, the lower part of a probably left horn core BM(NH) M 14536, part of a right horn core M 14537 and perhaps the base of a right horn core with part of the frontal M 29423. The first two London specimens were found in 1932 and are supposedly from Bed I. M 29423 is of unknown horizon ('? Bed I') and was found in 1931. These horn cores are not very curved backwards at the base, not mediolaterally compressed, have a flattened lateral surface and are less divergent than in *K. sigmoidalis*.

A left lower molar JK2 III B.FFM4-9 is larger than three teeth assigned to kob from the JK2 sites and could belong to a waterbuck.

MEASUREMENTS. Anteroposterior and mediolateral diameters at the base of the horn cores are:

EF-HR III–IV surface 068/6658	51·4 × 48·1
BM(NH) M 14536	55·3 × 47·3
BM(NH) M 29423	50·1 × 46·1

1

2

Plate 7

(Scale = 50 mm)

Fig. 1 ***Kobus kob.*** Lateral view of right horn core, JK2 GP8 III 1247.

Fig. 2 ***Kobus ellipsiprymnus.*** Lateral and anterior views of left horn core, EF-HR III–IV surface 068/6658. (Originally marked as from DK.)

COMPARISONS. A few horn cores from member K and the middle part of a horn core, F164-25 from member G, represent the waterbuck in the Shungura Formation, Omo.

A left upper molar BM(NH) M 25301, said to be of caprine type by Coryndon (1966 : 65), represents a waterbuck-sized reduncine in the Chiwondo Beds of Mwenirondo, Malawi. Its occlusal length is 21·9 mm.

Kobus kob (Erxleben 1777)

1965 *Kobus* sp. A Leakey : 47.
1965 *Kobus* sp. B Leakey : 47.

DIAGNOSIS. A species of *Kobus* smaller than waterbuck or lechwe; horn cores with some mediolateral compression, curving backwards at the base, inserted close together and fairly uprightly; large supraorbital pits; skull not wide; braincase angled quite strongly on the facial axis; occipital surface with an evenly rounded top edge; narrow mastoids often having a strong ventral rim in males.

REMARKS. Remains of kob are not very common at Olduvai Gorge. The larger *Kobus sigmoidalis/ellipsiprymnus* lineage occurs in Bed I sites other than FLKN, but disappears in Bed II after HWK EE. Thereafter in Bed II one finds much sparser remains of kob, although both kob and waterbuck occur in Bed III. The Olduvai kob need not be separated from the living species.

The skull, dentitions and partial skeleton of a kob were excavated from MNK middle Bed II in 1963. The skull, 104 + 106, is incomplete and unfortunately rather crushed but does show the reduncine lack of a preorbital fossa. It is hornless but has the slight horn core rudiments of a reduncine female. The auditory bullae are large and inflated. The mandibles, right 107 and left 108, and right maxilla 103 are considerably smaller than those of *Kobus sigmoidalis*. The premolar rows are incomplete, only P_4 being preserved on each side, but the molar rows are the size

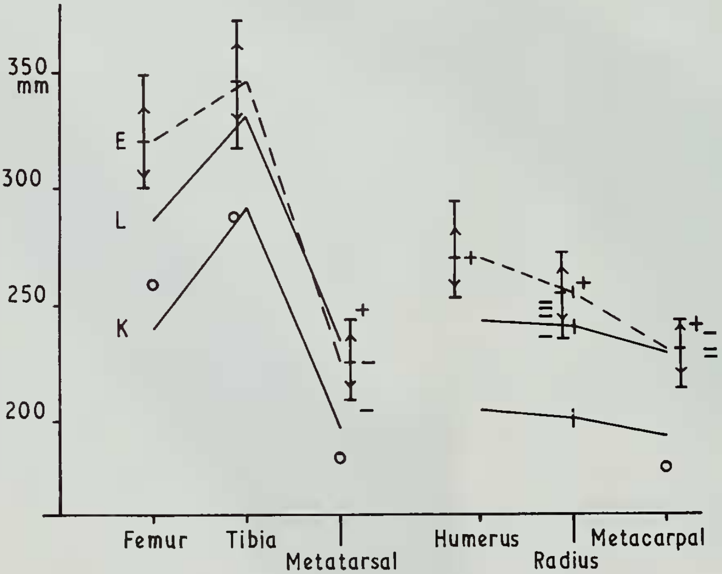

Fig. 13 Lengths of limb bones in Reduncini.

E = mean of 11 *Kobus ellipsiprymnus*, with ranges and standard deviations, L = a single *K. leche*, K = mean of 4 *K. kob*, O = the kob-sized reduncine from MNK II, + = reduncine from FLK I (humerus C 1092, radius C 1094, metacarpal C 1095).

Readings for other Bed I fossils are shown by the horizontal dashes; the relatively long metacarpals compared with the radii agree with the proportions of *K. leche* rather than *K. ellipsiprymnus*.

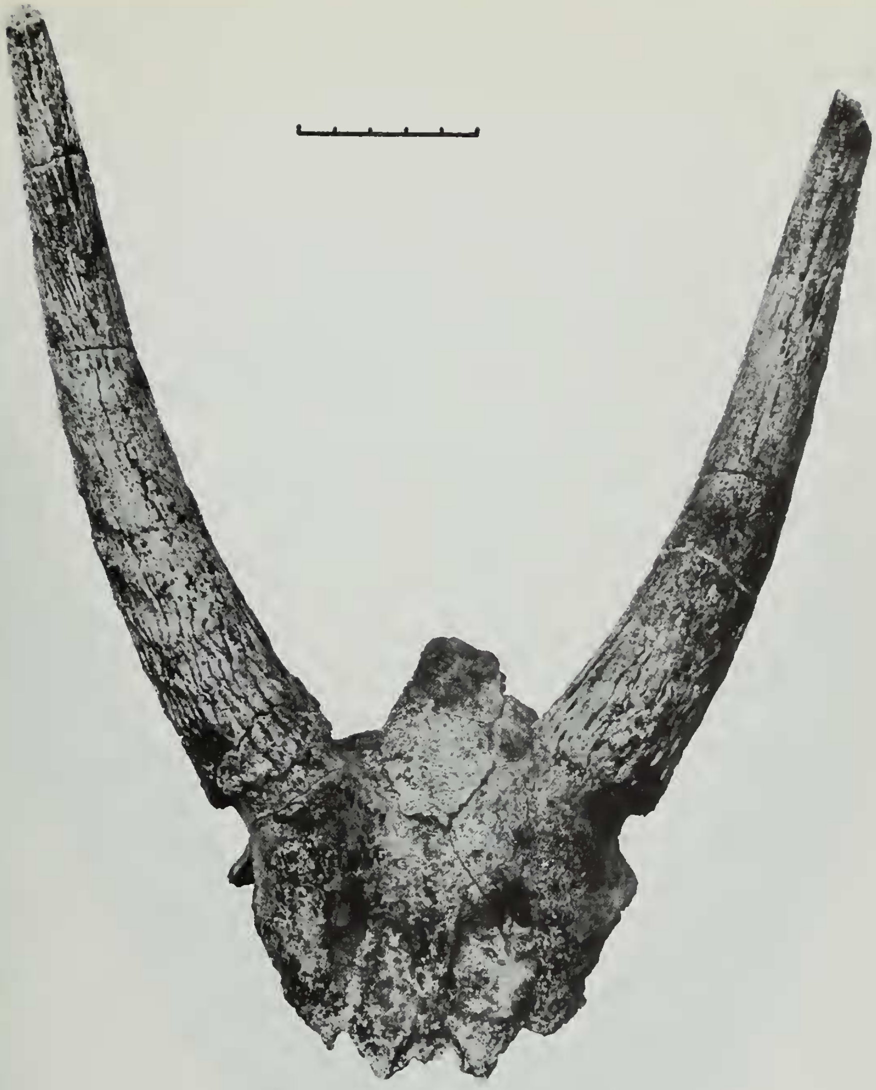

Plate 8 (Scale = 50 mm)

Kobus kob. Dorsal view of frontlet, ? MRC II 1962.068/6659.

of a lechwe or large kob. The upper teeth show less complicated central cavities and less accentuated and localized ribs between the styles than in living kob, but this difference might vanish after a little more wear. The skeleton preserved consists of the atlas vertebra 110 and a number of limb bones of the right side. These are the metacarpal 105, ulna 109, femur 101, tibia 102 and metatarsal 100. They fit a reduncine smaller than *K. sigmoidalis/ellipsiprymnus*. Identification as reduncine rather than tragelaphine is based on the slight medial tuberosity on the magnum–trapezoid facet of the metacarpal and posterolaterally a backwardly-pointed projection on the unciform facet, the fairly deep groove between the front and rear naviculocuboid facets and the poor anterior longitudinal groove on the metatarsal, and the deep hollows on the sides of the distal condyles of both the metacarpal and metatarsal. Their association with the skull and dentitions confirms this identification. Compared with four examples of living *K. kob* the femur of this individual is rather long and the metapodials rather short (Fig. 13); such proportions would not be surprising in an earlier kob.

Three Olduvai specimens give an indication of what the horn cores were like during Bed II times. These are a frontlet with complete horn cores 1962.068/6659 from upper Bed II (Pl. 8), a frontlet with incomplete horn cores P.P.R.1 from BK II East in 1953 (Leakey 1965 : 47, *Kobus* species A), and a left horn core SHK II 1957.579, a surface find (Leakey 1965 : 47, *Kobus* species B, said to be a right horn core but actually a left). 'GTC' is written on the first frontlet, which is inappropriate for its adherent Bed II matrix; however, the original inscription was MRC and this is a site near GTC at which Bed II does occur. These horn cores differ from living kob in being set quite obliquely in side view; they begin to curve upwards near the base and show less backward curvature at the base, being inserted quite widely apart and having very little mediolateral compression. The frontlet 1962.068/6659 is possibly sub-adult, and might have developed more basal backward curvature at a later age. The horn cores differ from those of *K. sigmoidalis* and *K. ellipsiprymnus* in being smaller, having less widely-set insertions and being less divergent: in addition the supraorbital pits are larger.

Two isolated reduncine teeth from Bed II are an appropriate size for the kob. These are left M$_3$s SHK II 1957.396 and BK II 1957.1362. A nearly complete left humerus BK II East 1953.442 and the distal end of a left humerus BK II 1957.42 are also likely to be of kob by their combination of slanted condyles with a deep hollow for the posterolateral humeroradial ligament.

The kob horn cores from Bed III differ from those of Bed II in being larger and longer, curving backwards at the base from a more upright insertion, and in having rather more mediolateral compression. They thus approach living kob more closely, but still differ in being larger, less uprightly inserted at the base and the insertions being less close together. The two specimens, both found at JK2 GP8 III in 1962, are a right horn core 1247 (Pl. 7, fig. 1) and a frontlet with complete left and nearly complete right horn core 068/6694 (Pl. 9). On the latter the backwardly curved basal part of the horn core is beginning to be a little less divergent than the middle part, which is an approach to the morphology of modern kob. These Bed III horn cores differ from those of *K. ellipsiprymnus* in being more curved back at the base, more compressed and probably less divergent, and 1247 shows quite a large internal sinus in its frontal extending into part of the pedicel. They are less divergent and have larger supraorbital pits than *K. megaceros*. They differ from *K. sigmoidalis* and *K. leche* in being less divergent and less mediolaterally compressed. An Olduvai horn core collected by Wayland in 1934, BM(NH) M 26928, is quite likely to belong here, but its horizon is unknown.

A right lower molar JK2 b III, a deciduous left P$_4$ JK2 III A.3271 M8, and a left M$_3$ JK2 GP8 III GN 47 are larger than the Bed II kob teeth but probably of the same lineage.

MEASUREMENTS. Measurements on the Bed II fossils are:

	SHK II 1957.579	BK II East P.P.R.1	? MRC II 068/6659
Skull width across posterior side of orbits	–	–	126·8
Length of horn core along its front edge	–	–	240·0
Anteroposterior diameter of horn core at its base	47·6	52·8	41·7
Mediolateral diameter of horn core at its base	48·8	45·9	41·5
Minimum width across lateral surfaces of horn core pedicels .	–	110·3	111·7
Width across lateral edges of supraorbital pits	–	60·1	57·1

Measurements on the MNK II specimen are:

Maxilla 103		Mandible 107	
Occlusal length M^1–M^3	50·2	Occlusal length M$_1$–M$_3$	53·9
Occlusal length M^2	17·6	Occlusal length M$_2$	17·4

Lengths and least thicknesses of the limb bones are:

Femur 101	259 × 24·0	Tibia 102	288 × 25·2
Metatarsal 100	184 × 19·4	Metacarpal 105	180 × 20·0

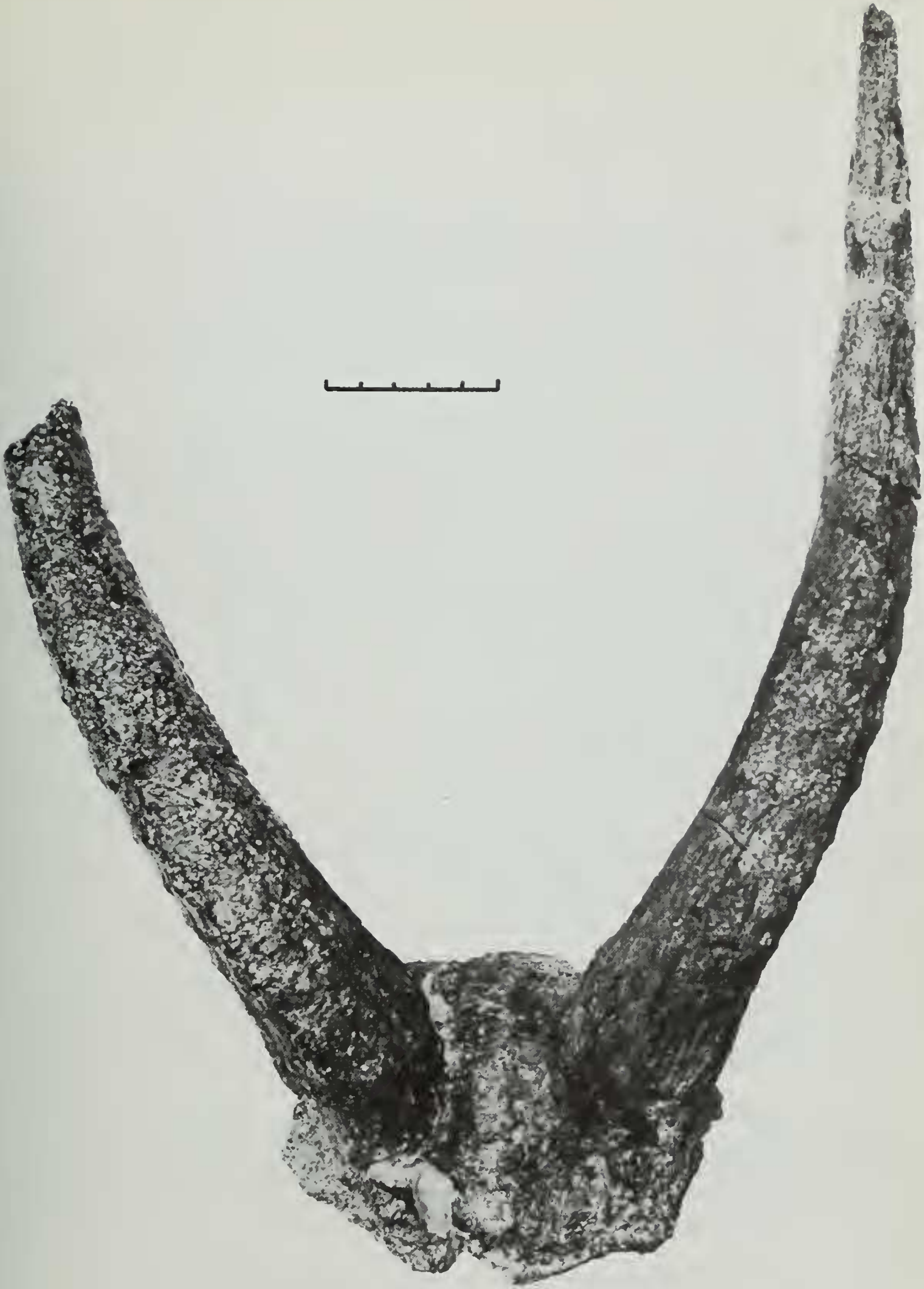

Plate 9 (Scale = 50 mm)

Kobus kob. Dorsal view of frontlet, JK2 GP8 III 068/6694.

Measurements on the Bed III fossils are:

	068/6694	1247
Length of horn core along its front edge	350·0	315·0
Anterposterior diameter at base of horn core	60·6	57·1
Mediolateral diameter at base of horn core	49·2	46·7
Minimum width across lateral surfaces of horn core pedicels	c. 122·5	–
Width across lateral edges of supraorbital pits	c. 56·8	–

COMPARISONS. The base of a reduncine horn core from Peninj, A67.238.1 (WN 64.227 TMG (lower) USC/MZ), is probably a kob like those of Olduvai Bed II.

The lower half of a left horn core from Rawe BM(NH) M 15936 is from a large kob, and has basal diameters of 54·2 × 48·2. This may have been the basis for the *Redunca* at Rawe recorded by Hopwood (*in* Kent 1942 : 124).

The base of a right horn core from Kanjera BM(NH) M 25628 probably belongs to a kob. It looks very modern with basal backward curvature and a flattened lateral surface. Its basal index is 46·1 × 36·7.

An Upper Pleistocene kob cranium with complete horn cores and associated palate M 15176 from Kazinga Channel, Uganda, was collected by V. E. Fuchs in 1931 (Hopwood 1939 : 314). It closely resembles living kob in the horn cores being long, with some mediolateral compression, inserted close together, curved back from the upright insertions, large and deep postcornual fossae, large supraorbital pits, a close approach of the temporal lines posteriorly, the occipital rather high instead of low and wide, no splaying of the anterior tuberosities of the basioccipital, strong ridges behind the anterior tuberosities, and inflated auditory bullae. The fossil differs from the living kob in its larger size, longer horn cores, the large mastoid without a strong ventral rim and the less evenly rounded occipital edge. Measurements on this cranium are as follows:

Length of horn core along its front edge	c. 380·0
Anteroposterior diameter at base of horn core	55·1
Mediolateral diameter at base of horn core	45·3
Minimum width across lateral surfaces of horn core pedicels	105·8
Width across lateral edges of supraorbital pits	51·9
Length from back of frontals to top of occiput	81·5
Maximum braincase width	83·2
Skull width across mastoids immediately behind external auditory meati	105·4
Occipital height from top of foramen magnum to top of occipital crest	46·9
Width across anterior tuberosities of basioccipital	29·0
Width across posterior tuberosities of basioccipital	42·0
Occlusal length M^1–M^3	46·2
Occlusal length M^2	15·8

Kobus kob is definitely known from high levels of the Shungura Formation, for example the Kaalam horn cores P.995-9, P.995-10 and P.996-10, as well as F.203-26 from member K and F.358-9 and F.409-6 from member L. Those from member L are notably large, like those of Olduvai Bed III, but somewhat stockier. There are some doubtful kob horn cores earlier in the Shungura Formation.

Two reduncine horn cores from the later fauna of the Kaiso Formation probably belong to the kob lineage; these are a weathered right horn core base BM(NH) M 12590 from Kaiso village (= cf. *Parmularius altidens* of Cooke & Coryndon 1970 : 212), and a right horn core base from Behanga I which appears to be the M 26622 of Cooke & Coryndon (1970 : 203). A right horn core base from Kanam East Hot Springs, one of two numbered M 15928, is probably also of this lineage.

There must also be mentioned the horn core thought to be BM(NH) M 26623 from Kaiso village, and referred to elsewhere in this paper (p. 414). It has hitherto been taken as alcelaphine, but the lack of a sinus system in the preserved part of its pedicel suggests that it may be a reduncine. Its assignment would thus be ? *Kobus* sp.

Potentially very interesting is the late Pleistocene horn core from Abu Hugar, Sudan, figured by Bate (1951 : text-fig. 3) which Wells (1963 : 303) discussed and identified as cf. *Kobus* sp.

BM(NH) M 21698 is a cast of it. It looks reduncine but is too large and too compressed mediolaterally to fit easily into any living species. The upright insertion in side view, backward curvature and large supraorbital pit suggest that it could be related to *K. kob*, although we have seen nothing like it from elsewhere. Its basal diameters are 61·4 and 40·7 mm.

Reduncine fossils with kob-like characters are well known in the Pinjor Formation of the Siwaliks, and also occur in the preceding Tatrot and Dhok Pathan. The cranium BM(NH) 39559a of *Vishnucobus patulicornis*, already mentioned in the discussion of *Kobus sigmoidalis*, is not unlike a kob. Conspecific pieces would be the holotype frontlet in Calcutta and the holotype cranium of *Indoredunca sterilis* Pilgrim (1939 : 113) also in Calcutta. Other Pinjor reduncines are a little more kob-like and have mostly been classified as *Sivacobus palaeindicus* (Lydekker) by Pilgrim (1939 : 99). We believe that they could be a separate species. They comprise a cranium BM(NH) 39559, and two other more nearly complete skulls with horn cores broken at the bases of their pedicels, M 487 and M 2402, the last one being the holotype. Another male cranium, 17437, is conspecific with the material of *Sivacobus palaeindicus*, although previously regarded as *Vishnucobus patulicornis* (Pilgrim 1939 : 103, mistakenly giving the registered number as 17237). *S. palaeindicus* agrees with *V. patulicornis* in having horn core insertions close together, large supraorbital pits also close together, and strong temporal ridges and fairly small mastoids. However, 39559 has horn cores more massive and with less divergence than 39559a. M 2402 and 17437 differ from the other pieces by their more angled and narrower braincase and by each side of the occipital surface facing laterally as well as backwards. The auditory bullae are large in 17437 but appear to be smaller in M 2402. The closeness of the horn bases and the supraorbital pits to the mid-line of the skull and the large size of the supraorbital pits are much as one might expect in kob ancestors, and M 2402 and 17437 are still more kob-like in their narrower and more angled braincases. However, we do not know whether even the more kob-like examples are ancestral to kobs. They may only be earlier members of the same lineage as *Vishnucobus patulicornis* and kob-like by reason of their relative primitiveness. Could Indian populations of antelopes as closely associated with proximity to water as the reduncines have been connected across Arabia with African populations as late as Pinjor times? Does the retention of strong temporal ridges on the cranial roofs of the Pinjor reduncines suggest that they are earlier than *Kobus sigmoidalis* as known back to Shungura member C, or that they are an endemic Indian group? If they were endemic, the chances would be lessened that the were congeneric with *Kobus*.

Gangicobus asinalis Pilgrim (1939 : 111) and *Sivadenota biforis* Pilgrim (1939 : 105) were founded for two hornless female skulls, BM(NH) 36673 and 39569 respectively, but it is impossible to decide to which of the above two species, *Vishnucobus patulicornis* and *Sivacobus palaeindicus*, they should be allocated. It is interesting that M 487 and M 2402, but not the female skulls, retain small preorbital fossae which have disappeared in living reduncines. These fossae are further reduced in the Omo *Menelikia lyrocera* and absent in the females of the Olduvai *Kobus sigmoidalis* and the Bed II kob, but the condition in other fossil reduncines is unknown. The occurrence of the Siwaliks reduncines in the same area as earlier abundant boselaphines and their strong temporal ridges suggest that they could have a boselaphine ancestry. The Tatrot and Dhok Pathan reduncines are smaller and less adequately preserved, but presumably they were ancestral to those of the Pinjor. No Siwaliks reduncines resemble *Redunca* or *Menelikia*.

Baard's Quarry at Langebaanweg, South Africa, yielded some horn cores wrongly assigned by Gentry (*in* Hendey 1970a : 115) to *Redunca ancystrocera*. They are only a little mediolaterally compressed, inserted fairly obliquely and divergently, have slight backwards curvature, a flattened lateral surface, no transverse ridges, and moderate-sized but very deep postcornual fossae. They are very like the Tatrot and Dhok Pathan reduncines except that their supraorbital pits are smaller.

Genus *REDUNCA* H. Smith 1827

Type species. *Redunca redunca* (Pallas 1767).

Generic diagnosis. Reduncines frequently smaller than *Kobus*; skulls low and wide; horn cores of variable length but always with an upwards curvature which is forwardly concave from the base, with little mediolateral compression, and often with a posteromedial or medial flattened surface near the base; frontals without internal sinuses; anterior tuberosities of the basioccipital very large and outwardly splayed.

Remarks. *Redunca* is a smaller and less diversely adapted genus than *Kobus* and this allows a diagnosis with more characters.

Redunca sp.

Remains of *Redunca* are very scarce at Olduvai. Reduncine right lower molars DK I 067/4085 and FLKN I 067/185 are small enough to fit *Redunca*. A left upper molar JK2 III A.1438N is also probably *Redunca*, but could just possibly be a kob.

Comparisons. Complete and fragmentary left horn cores BM(NH) M 26930 and M 26931 from Kanam East and an immature right one M 26932 from Kanam belong to *Redunca*. M 26930 retains the midfrontals suture, is set obliquely in side view, has a flattened posteromedial surface near its base and is short and little divergent. All three horn cores are distinguishable from *R. redunca* only by being less curved in side view. A mandibular fragment with a left lower molar M 15934 from Kanam Central is of *Redunca* size. The more complete of two horn cores numbered M 15928 from Kanam East Hot Springs differs from M 26930 by having less anteroposterior compression and a more medial position of the flattened posteromedial surface. These characters look primitive and M 15928 may be assigned to *Redunca ? darti* (see below), yet the Hot Springs fossils are thought to derive from the Rawe beds later than the Kanam beds (Kent 1942 : 124).

M 25634 is a right horn core base of *R. redunca* from Kanjera, but it appears to be little fossilized. M 25713 is a little-fossilized left upper molar of *Redunca* size from Kanjera.

Teeth small enough for *Redunca* are scarce in the Shungura Formation, Omo, e.g. left lower molar L.32-179 from member C and left lower premolar L.209-4 from member E.

Reduncine molars M 26620 and M 26621 (Cooke and Coryndon 1970 : 203) from the later Kaiso faunal assemblage at the Behanga locality are small enough to belong to *Redunca*, but of the two further teeth from Makusa mentioned by these authors, one is a larger reduncine and one is an alcelaphine.

In contrast with Olduvai, remains of *Redunca* are fairly common in South Africa and occur at several fossil sites. *R. arundinum* is the commonest antelope at Melkbos (Hendey 1968 : 110) and similar remains occur at Swartklip (Hendey & Hendey 1968 : 51; pl. 2). At Elandsfontein parts of a skull 20039, several frontlets, horn cores and mandibles represent the apparent ancestor of living *R. arundinum*, but have horn cores more anteroposteriorly compressed, less divergent and possibly shorter. The short and little-divergent horn cores happen to resemble *R. redunca*, but since the occipital surface has a more rounded edge like *R. arundinum* and since *R. redunca* is a more northern form, this probably shows only that earlier members of the *arundinum* lineage were less remote from *redunca* than is the living *arundinum*.

The Elandsfontein subspecies of *R. arundinum* is possibly descended from the Makapansgat Limeworks *R. darti* Wells & Cooke (1956 : 17, figs 7–9). This extinct species differs from *R. redunca* and *R. arundinum* in its horn cores being less oblique in side view, and the posteromedial flattened surface lying more medial than posterior. It differs from *R. fulvorufula* in its larger size and horn cores relatively larger, more divergent, more obliquely inserted, and with posteromedial or more medial flattenings on the surface. Unlike any living *Redunca* it probably had a small preorbital fossa, as seen on the incomplete skull BPI M.690 and partial face M.2798. Whether *R. darti*, being tentatively ancestral to *R. arundinum*, was also ancestral to *R. redunca* is not known. The Kanam East Hot Springs horn core BM(NH) M 15928, mentioned above, is similar to *R. darti*.

Arambourg (1938 : 44; pl. 8, figs 1–2) recorded *Redunca redunca* from the late Pleistocene and early Holocene of north-west Africa. The horn cores of similar age figured as *Antilope* (*Oegoceros*) *selenocera* Pomel (1895 : pl. 6, figs 1–3) are also assignable to *R. redunca*. They do not represent a waterbuck as Joleaud (1936 : 179) believed. Arambourg (1957 : 51) pointed out that the frontlet *A.* (*Dorcas*) *triquetricornis* Pomel (1895 : 28; pl. 11, figs 1–2) is also a *Redunca* which most probably went with the teeth called *A.* (*Nagor*) *maupasii* Pomel (1895 : 38; pl. 10, figs 1–11). The size, inclination and cross-sections of the *Redunca* horn cores figured by Pomel forbid their assignment to *R. fulvorufula.* Coppens (1971 : 53) refers to a *Redunca* from Villafranchian-equivalent deposits of Garaet Ichkeul and Hamada Damous, Tunisia, but the details are to be published later.

Redunca ancystrocera Arambourg (1947 : 416, fig. 62; pl. 29, fig. 4; pl. 31, figs 2, 4, 4a) from the Shungura Formation, Omo, is ill-suited as a *Redunca* on account of its larger size and horn cores often with posterolateral keels and flat lateral surfaces. It seems better classified as a species of *Kobus.* Its horn core characters of low insertion angle, great divergence and pronounced upwards and forwards curvature at the tips resemble living *Redunca* but are unlike the more primitive fossil species *R. darti.*

The Laetolil right horn core which Dietrich (1950 : 36; pl. 2, fig. 21) called 'Reduncini gen. et sp. indet.' is more likely to be alcelaphine (see p. 382).

Genus *THALEROCEROS* Reck 1935

1935 *Thaleroceros* Reck : 218.

Type species. *Thaleroceros radiciformis* Reck 1935.

Generic diagnosis. There is only one species in the genus.

Thaleroceros radiciformis Reck 1935

1935 *Thaleroceros radiciformis* Reck : 218, fig. 2.
1937 *Thaleroceros radiciformis* Reck : 142; pl. 8.
1950 *Alcelaphus radiciformis* Dietrich : 15, 33.

Diagnosis. A large antelope; horn cores fairly long but very massive, not very compressed mediolaterally, without a flattened lateral surface, without keels or transverse ridges, diverging very little, with an upwards and forwardly concave curvature from the base, and a sudden diminution of cross-sectional area near their tip; horn core pedicels united to form a single massive structure without internal sinuses and with paired protuberances anteriorly just below the horn core bases; postcornual fossae poorly marked; orbital rims slightly projecting; supraorbital pits small and elongated; frontals internally hollowed at the level of the supraorbital pits.

Holotype. The holotype and only known specimen is in Munich, where it has survived the Second World War. It is a frontlet with right horn core, marked 'VI 306, 1931 II 101'.

Horizon. Reck (1937 : 138) thought the fossil came from Olduvai Bed IV. R. L. Hay (personal communication, September 1969) identified matrix from it as 'a pale brown sandy clay, not at all diagnostic in locating the specimen's horizon. It could have come either from Bed II (probably the upper part) or from Bed IV.'

Remarks. The holotype has an almost complete right horn core, but with some plaster restoration near its tip on the medial side and an artificial hole posteromedially near its base. Both supraorbital pits, the upper parts of both orbits, the anterodorsal part of the braincase roof and a small part of the right lateral wall are preserved. The left horn core has been restored in plaster.

The pedicel is higher at the front than at the back, and there is a shallow concavity below and between the anterior protuberances. Posteromedial breakage on the right side of the horn pedicel shows that it is spongy within, and the hollowing of the frontals is therefore restricted to a more anterior level, which is unlike the alcelaphine condition. The posteromedial hole near the base of the right horn core shows that the horn core itself is spongy within, and therefore unlike Caprini. The right protuberance on the pedicel is larger than the left one, and the base of the right side of the pedicel is more swollen posteriorly. Possibly the missing left horn core was smaller than the right one, and the animal perhaps old.

The left horn core 1955 P.P.F.4 from the surface of FLK tentatively assigned by Leakey (1965 : 65; pl. 88) to *T. radiciformis* is not this species but an unidentified alcelaphine (p. 393).

MEASUREMENTS. Measurements on the frontlet of *Thaleroceros radiciformis* are:

Length of horn core along its front edge	306·0
Anteroposterior diameter of horn core at its base	121·0
Distance from horn core tip to centre of protuberance	254·0
Minimum width across horn core pedicel	119·4
Width across lateral edges of supraorbital pits	67·0
Maximum width across fossil and restored horn core bases	*c.* 198·0

COMPARISONS. *T. radiciformis* shows a distant resemblance to *Kobus ancystrocera* (Arambourg 1947 : 416) from the Shungura Formation, Omo, in its forwardly curved horn core tip and upright horn core pedicel, and a horn core base of the latter, L1-153 from member B of the Shungura Formation, Omo, even has a localized protuberance at the top of its pedicel. It is possible that *T. radiciformis* is a very specialized descendant of *K. ancystrocera*, but it is much larger, the pedicel is united, and the horn cores do not diverge so strongly. Possible intermediates are a complete right and part of the left of a pair of horn cores, BM(NH) M 15925, from Kanam. They are supposed to have come from a site called 'Museum Cliff'. They are considerably larger than *K. ancystrocera* and less mediolaterally compressed than either *K. ancystrocera* or *T. radiciformis*. Their horn core index is 70·2 × 60·2 mm. However, they do not attain the size of *T. radiciformis*, and their pedicels have not become united, so they are a good intermediate stage. M 15927, labelled '*Cobus* sp.', from Kanam East Hot Springs is another piece of horn core which is very like the pair M 15925. Reck (1937 : 142) had noticed similarities between *T. radiciformis* and the reduncines, but was deterred from suggesting a relationship by the huge united pedicel and by the internal hollowing of the frontals.

Tribe **HIPPOTRAGINI**

The living Hippotragini comprise the sable, roan, oryx and addax. The first lives in woodland, the second in clearings or along the edges of woodland, the oryx in drier habitats and the addax in the Sahara desert. They are large, rather stocky, mainly grazing (except the addax) antelopes with large, unkeeled horns (spiralled in the addax) and moderately hypsodont teeth. The distinctive skulls characters are: horn cores moderate to long, horn cores not very divergent and without keels or transverse ridges, horn core pedicels hollowed, both sexes with horns. Postcornual fossae shallow when present, braincase long, midfrontals suture moderately complicated, parietofrontals suture straight and not very complicated, temporal lines not approaching very closely, ethmoidal fissure present, infraorbital foramen fairly high over the P^2–P^3 junction, premaxillae with a short contact along the sides of the nasals, nasals without lateral flanges anteriorly, median indentation at the back of the palate more or less level with the lateral ones, mastoid exposure moderate to large, foramina ovalia large, auditory bullae moderately large. Teeth large relative to the jaw size, upper molars with basal pillars, lower molars with goat folds anteriorly, P_4s without metaconid and paraconid fusion to form a complete medial wall at the front of the tooth, and mandibles with deep horizontal rami.

Hippotragus leucophaeus (Pallas 1766), the blaauwbok of southern South Africa, was the smallest of the three *Hippotragus* species. It became extinct at the end of the 18th century. It is the type species of *Hippotragus*.

Hippotragus equinus (Desmarest 1804) is the roan antelope of much of Africa south of the Sahara.

Hippotragus niger (Harris 1838), the sable antelope of East and South Africa, differs from *H. equinus* in relatively larger, longer, more mediolaterally compressed and more uprightly inserted horn cores, frontals more raised between the horn core bases, narrower skull width across the orbits and a shorter braincase which is more bent on the facial axis.

Oryx gazella (Linnaeus 1758), the gemsbok and beisa of South and East Africa, differs from living *Hippotragus* in having a lower and wider skull, and straighter and less compressed horn cores, inserted very obliquely, further behind the orbits and wider apart. The gemsbok has larger teeth than the beisa.

Plate 10

(Scale = 50 mm)

Hippotragus gigas

Fig. 1 Anterior view of immature partial cranium, DK I 067/5496.

Fig. 2 Lateral view of left horn core, FLK II 1961.068/6663.

Oryx dammah (Cretzschmar 1826), the scimitar oryx of west Africa, has more curved horn cores than other *Oryx*.

Oryx leucoryx (Pallas 1777) is the slightly smaller Arabian oryx.

Addax nasomaculatus (Blainville 1816) is the spiral-horned addax which lives in parts of the Sahara desert. It is still more adapted to life in arid regions than oryxes, and no fossils are known.

Genus ***HIPPOTRAGUS*** Sundevall 1846

Type species. *Hippotragus leucophaeus* (Pallas 1766).

Generic diagnosis. Horn cores mediolaterally compressed, strongly curved backwards, inserted uprightly above the orbits and closer together than in *Oryx*; ethmoidal fissures blocked by bone internally; nasals more domed than in *Oryx*; mastoid facing partly laterally as well as backwards; longitudinal ridges behind the anterior tuberosities of the basioccipital are stronger than in *Oryx*; lower molars with stronger goat folds than in *Oryx*.

Hippotragus gigas L. S. B. Leakey 1965

1942 *Hippotragus equinus* Hopwood (*in* Kent) : 126.
1965 *Hippotragus gigas* Leakey : 49; pls 56, 58–61.
1965 *Hippotragus* cf. *equinus* (in part) Leakey : 51.
1965 Bovinae indet. Leakey : 66(a); pls 89–90.
1965 cf. Alcelaphini Leakey : 66(c).

Diagnosis. A species larger than living *Hippotragus* at least during part of the Olduvai sequence; males with very large and long horn cores; horn cores less mediolaterally compressed than in the sable and probably less than in the roan; a shorter basioccipital than in living *Hippotragus*; braincase proportions low and wide as in the roan rather than high and narrow like the sable, but less long than in the roan; frontals not raised between the horn corn bases as in the sable but resembling the roan; outbowings not accentuated nor localized on lateral walls of upper molars or medial walls of lowers; upper molars without large Y-shaped basal pillars; lower molars with large goat folds as in living *Hippotragus* but without pinching of the lateral lobes; premolar rows as short and P_2s as small as in *Oryx*.

Several crania from Elandsfontein are of a large hippotragine which seems conspecific with *H. gigas* and from this material a further character can be added to the diagnosis: large foramina ovalia.

Holotype. Incomplete cranium with both horn cores F.3662 068/5812 P.P.T.2 in the Nairobi collections.

Horizon. The holotype comes from Bed II, Olduvai. According to R. L. Hay (personal communication, September 1973) a small remaining piece of matrix was limestone with sand-sized volcanic detritus indicating an origin above the Lemuta Member, probably in the eastern half of the Main Gorge. Other specimens are moderately common in Beds I–III. The species is known from Kanjera and Peninj, from the Chiwondo Beds in the Karonga District of Malawi, and in South Africa from Makapansgat Limeworks, Elandsfontein and possibly Florisbad.

Remarks. *H. gigas* is the only species of *Hippotragus* at Olduvai. It had a long history in East Africa and continued into the late Pleistocene in South Africa. The later stages were certainly not ancestral to living *Hippotragus*, but we do not know when the lineages separated. The more complete remains from Olduvai are a juvenile cranium with both horn cores DK I 067/5496 (Pl. 10, fig. 1), a cranium with horn cores, both mandibles (Pl. 11, fig. 3) and parts of the maxillae FLKNN I 608 (thought to be possibly alcelaphine by Leakey (1965 : 66(c)), the female paratype cranium with horn cores 1957.56 P.P.T.3 from VEK at the top of Bed I, a complete left horn core and part of the braincase 1961.068/6663 from FLK middle Bed II (Pl. 10, fig. 2), the back of a skull TK II 067/5310, a complete left horn core BK II 1963.3042, and a frontlet with the basal part of the right horn core F.3014 of unknown stratigraphic position (Leakey 1965 : 66(a); pls 89–90). Specimens in London are the lower part of a left horn core BM(NH) M 14530 from Bed I

1

2

3

4

Plate 11

(Scale = 25 mm)

Fig. 1 *Pelorovis oldowayensis.* Right M_3 and right upper molar, HWK East II 2688 and 2687.

Fig. 2 *Syncerus acoelotus.* Right dP_2–M_1 with erupting M_2, BK II Extension 1953.77.

Fig. 3 *Hippotragus gigas.* Lower jaws with cleaned right P_2–M_3, FLKNN I 608.

Fig. 4 *Hippotragus gigas.* Left M^2–M^3, BK II 1963.2226.

and a right horn core base M 21449 from Bed II (written on the horn core and in the register) or Bed I (written on the label), both found in 1932 and recorded as *H.* cf. *equinus* by Leakey (1965: 51), a right horn core M 21448 from Bed II in 1931 (Leakey 1965: 50; pl. 61), a left horn core M 29425 from the surface of GHTK II in 1935 and the lower part of a left horn core M 29424. Possibly belonging to this species are pieces of horn core M 14541 and M 14533 both found in Bed I in 1932.

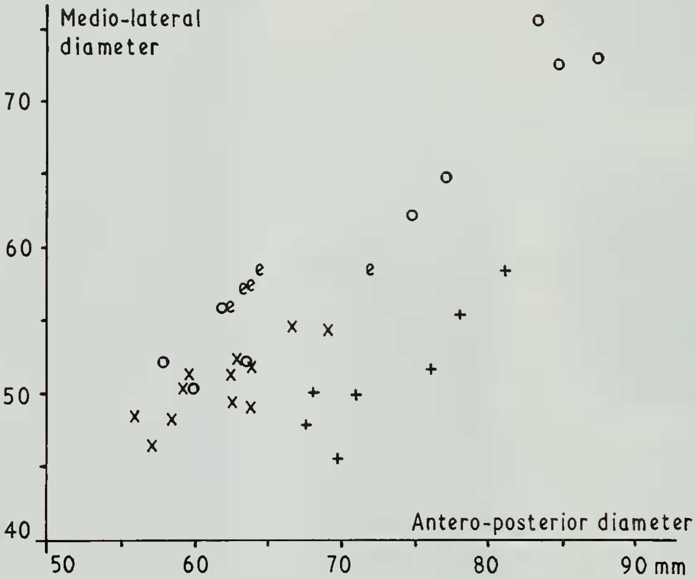

Fig. 14 Horn core dimensions of *Hippotragus*.

o = *H. gigas* from Olduvai Gorge, *e* = *H. gigas* from Elandsfontein, x = *H. equinus*, + = *H. niger*.

All readings are from males or individuals which cannot be reliably distinguished from males. *H. gigas* shows great variations in size, although its lowest reading, BK II East 1953 P.P.R.5, is probably not adult.

The holotype cranium is definitely larger than either of the living species and it has horn cores larger and longer than those of the roan, both absolutely and in relation to skull size. The dimensions of the horn cores probably exceed those of all but the largest sable. The other Olduvai horn cores are also larger and longer than in living species, and the young cranium from DK I is also rather large. The horn cores of *H. gigas* are less compressed than in sable and probably than in roan (Fig. 14), little divergent in anterior view (except in 608), inserted above the back of the orbits, and lack a flattened lateral surface, keels and transverse ridges. The various horn cores from Olduvai are consistent with the supposition that the adult females and the young of both sexes have more obliquely inserted horn cores than adult males and that those of females have less backward curvature than males. This is what happens in living *Hippotragus*. Thus the horn cores of 067/5496, which is young, are inserted obliquely; those of 608, probably a female, are inserted obliquely and lack much backward curvature; those of the paratype, also probably a female, also lack much backward curvature but are not inserted very obliquely; that of 068/6663 is obliquely inserted but quite strongly curved backwards and could have belonged to a male whose horns had not yet attained full size.

There seem to be no postcornual fossae in *H. gigas*. That part of the frontals constituting the horn core bases is clearly hollowed, but as seen on the holotype and probably the paratype and 067/6663 the frontals are not raised between the horn core bases as in the sable but are like the

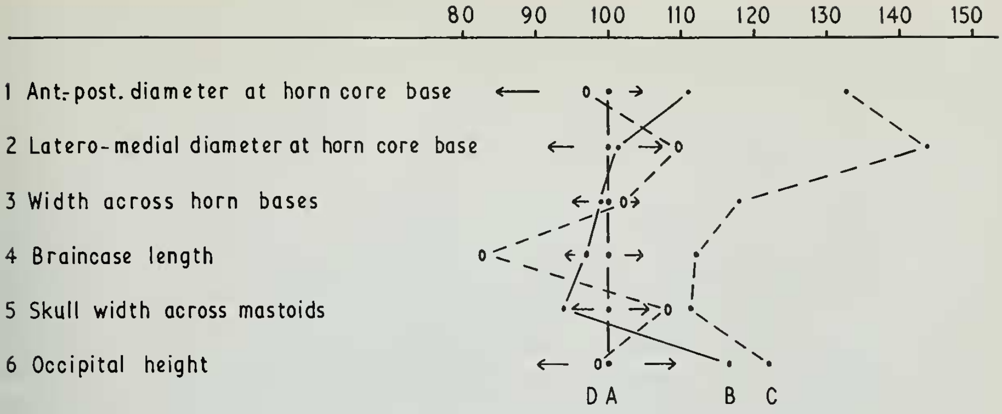

Fig. 15 Percentage diagram of skull measurements in *Hippotragus*.

A = standard line at 100% for mean of 12 male *H. equinus*, B = mean readings for 7 male *H. niger*, C = *H. gigas* holotype, D = mean readings for 3 *H. gigas* from Elandsfontein.

Horizontal arrows show the standard deviations for *H. equinus*. Braincase length is measured from the back of the frontals to the occipital top.

roan. The supraorbital pits are small and about as wide apart as in living hippotragines. In side view the tops of the orbits are close under the tops of the horn core pedicels. The midfrontal and parietofrontal sutures are complicated and there is but little central indentation of the parietofrontal suture.

The braincase sides of *H. gigas* are parallel or widen posteriorly. The braincase proportions, as shown by the holotype, paratype and 067/5496, are relatively wide like the roan but relatively less long (Fig. 15); that of 608 appears still shorter but has been considerably crushed anteroposteriorly. The occipital surface faces backwards and the median occipital ridge is slightly developed. On the holotype and 067/5496, though not on 067/5310, there are shallow hollowings on either side of the median vertical line at the top of the occipital surface which are not convincingly present in either of the living species, though there may be indications in the roan. The nuchal crest is moderately prominent on the holotype and 067/5310, though this is not noticeably

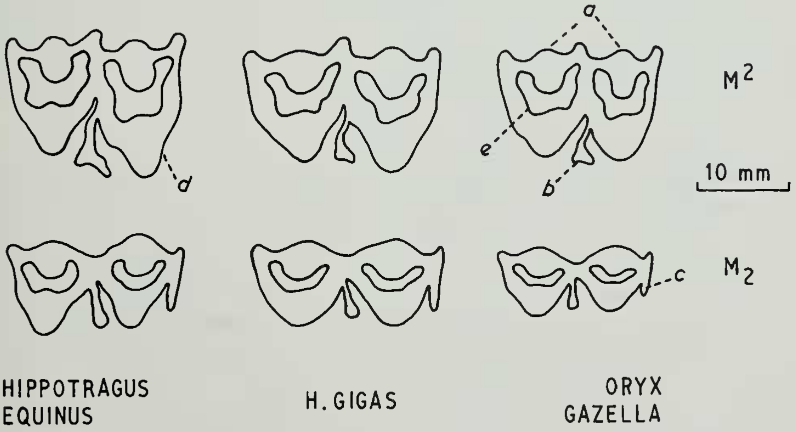

Fig. 16 Occlusal surfaces of right upper and lower molars in some hippotragine species. The anterior direction lies to the right of the page. *a* = ribs, *b* = basal pillar, *c* = goat fold, *d* = constriction of lobe, *e* = outline of central cavities.

different from the living species. The basioccipitals of 608, 067/5310, the paratype and probably the holotype are shorter than in the living species. There is very little of a central longitudinal groove on the basioccipitals. The anterior tuberosities of the basioccipital are almost as wide as the posterior ones. The anterior tuberosities of 608, 067/5310 and the paratype can be seen to be localized, as in oryx rather than sable or roan. The mastoid exposure in *H. gigas* is large.

All the hippotragine teeth at Olduvai can be taken as belonging to *Hippotragus gigas* (Fig. 16). In this connection, the skull FLKNN I 608 is important in providing the only association between dentitions and horn cores, and one has to be certain of the specific identity of 608. It is likely that distortion has forced the braincase roof close against the back of the horn cores, making them appear very obliquely inserted as in oryxes. However, 608 cannot be an oryx because the horn cores are too large, they are too backwardly curved, they do not taper rapidly above the base like a fossil oryx horn core FLK I G.390, the pedicel top is probably too far above the orbit and the orbital rim probably projects too little. The skull can therefore be taken as *H. gigas*.

The teeth of *Hippotragus gigas* are about the size of living *H. equinus* or slightly larger at least from middle Bed II times onwards. They resemble living *Hippotragus* in the large size of the goat fold, but otherwise they are more like *Oryx* in the poorly emphasized outbowings of the lateral wall of the upper molars and the medial wall of the lowers, the lack of large Y-shaped basal pillars on the upper molars, the lower molars without pinching of the lateral lobes, the shorter premolar row, and perhaps in the less complicated outline of the central cavities. Thus the teeth of *H. gigas* are more primitive than in living roan or sable, and with premolar rows as short as in *Oryx* (Fig. 17) they are almost indistinguishable from oryx.

There is little definite sign that these characters are becoming more advanced in the sparse fossils from middle or upper Bed II. However, the maxilla BK II 1963.2226 (Pl. 11, fig. 4) does have upper molars with rather localized and accentuated ribs between the styles. In Bed III the lower molar JK2 A.2838 is still primitive, but JK2 A.3028 begins to show some constriction of the

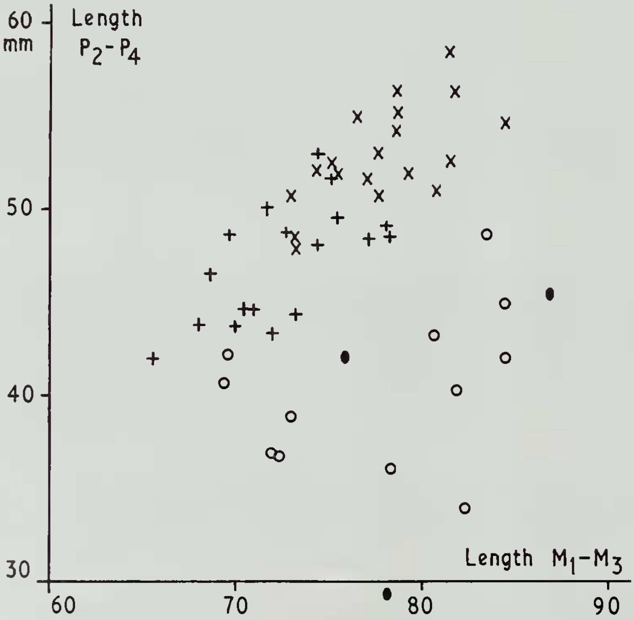

Fig. 17 Proportions of lower premolar and molar rows in some hippotragines.
o = *Oryx gazella*, + = *Hippotragus niger*, x = *H. equinus*.
Solid circles show *H. gigas*, the smaller one being FLKNN I 608 from Olduvai, and the larger the mean of 2 premolar rows and 6 molar rows from Elandsfontein. A molar row reading for *H. gigas* FLK I 1960.067/1097 is also shown below the horizontal axis.

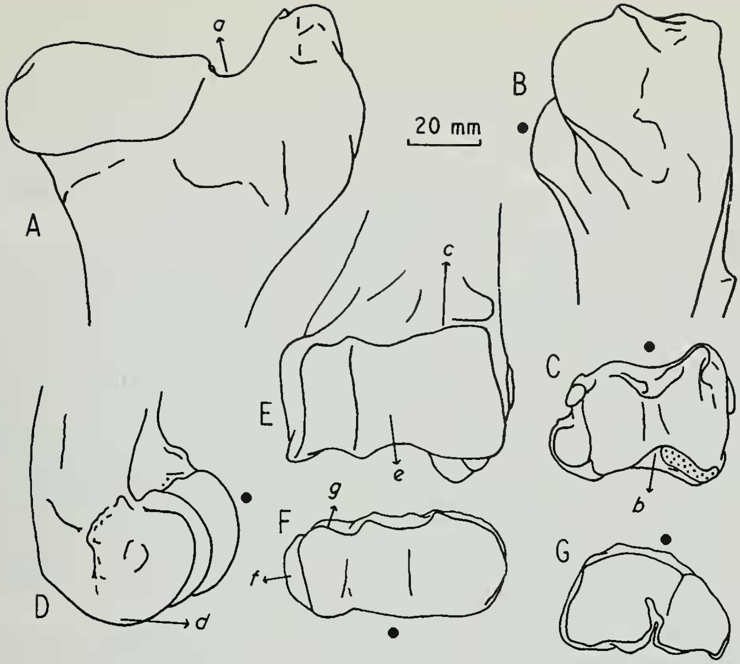

Fig. 18 Limb bones of Olduvai *Hippotragus*. (Solid dots show anterior sides.)

A, B. Anterior and lateral views of proximal left femur FLKNN I 800.
C. Distal articular surface of right tibia of same skeleton.
D, E. Lateral and anterior views of distal right humerus of same skeleton.
F. Proximal articular surface of right radius of same skeleton.
G. Proximal articular surface of right metacarpal FLKNN I 960.

a = hollow between great trochanter and articular head which is less deep than in alcelaphines.
b = shallow rear indentation into distal articular surface,
c = no indentation at top of medial condyle,
d = rounded ventral edge of lateral side,
e = medial groove insufficiently deep to match alcelaphines,
f = small lateral tubercle,
g = back of lateral facet set posteriorly.

These characters may be compared with the alcelaphine limb bones shown in Fig. 23, p. 374.

lateral lobes, while the right lower molar fragment from JK2 has a localized and accentuated rib on its medial wall. We need more evidence about whether or not *H. gigas* teeth become more advanced later in the Pleistocene. (A deciduous P^4, BK II 1952.167, is so markedly advanced that one must doubt whether it is contemporary with its alleged horizon.)

It is rather difficult to distinguish teeth of *Hippotragus gigas* from those of the bovine *Syncerus acoelotus* or its ancestor in Olduvai Beds I and II. Some general guides can be laid down. Hippotragine teeth can be expected to be a little smaller and the premolar rows very short. The lower molars may have less narrowed lateral lobes, less pronounced outbowings on the medial walls, and goat folds which extend down to the neck of the tooth. Bovini too may occasionally have goat folds, as in BK II 1953.067/5230, but they are smaller and disappear before the tooth is completely worn down. The hippotragine P_4 has a large bulbous metaconid (more so than in living *Hippotragus*) and there is no tendency to fuse paraconid and metaconid. The identification of hippotragine upper molars is still more difficult, but one can look for less mediolateral width lower down and the correlated character of less curved central cavities.

H. gigas seems closer to the roan than to the sable in the low and wide braincase, not very compressed horn cores, projecting orbital rims and lack of raised frontals between the horn core bases. It differs from the roan in the much larger horn cores, probably less long braincase, sometimes stronger temporal lines, shorter basioccipital, less development of longitudinal ridges behind the anterior tuberosities of the basioccipital and larger foramina ovalia. Morphologically, *H. gigas* could be ancestral to either or both living species of *Hippotragus*, except that its very short premolar row would be a problem. It is entirely possible that some populations of *H. gigas* gave rise to living *Hippotragus*, while elsewhere the species *gigas* lived on.

The partial skeleton of a large bovid was found at the base of the tripartite level of FLKNN I in 1961. This is slightly higher in the sequence than level 1 of FLKNN I and is overlain by Tuff ID (M. D. Leakey 1971b : fig. 19). The skeleton (Figs 18 and 19) consists of a complete right humerus 800M, complete right radius 800D and right ulna 800P, complete right tibia 800, complete left femur 800A, most of the pelvic girdle 800H–J, right calcaneum 800L and several vertebrae and ribs. The remains are those of a hippotragine and are distinguished from a similar-sized large alcelaphine (though with more difficulty than might be expected from such complete material) by the following characters: in anterior view the hollowing between the great trochanter and articular head of the femur is not quite deep enough, the radius and tibia are too short, there is a middle patellar groove at the top of the cnemial crest of the tibia, the rear indentation into the distal articular surface of the tibia is too shallow, there is no indentation on top of the medial condyle distally on the humerus and no V-projection distally on its lateral surface, the medial groove distally on the humerus is insufficiently deep, and on the radius the lateral tubercle is too small and the back of the lateral facet is not set anteriorly.

The anteroposteriorly long lateral part of the femur articular head and lack of extreme forward extension of the great trochanter can be seen in living *Oryx* rather than *Hippotragus*. The extreme forward projection of the medial side of the patellar fossa on the femur and the raising of the lateral edge of the lateral facet on the tibia are also more *Oryx*-like. The skeleton is probably *Hippotragus gigas* but shows some *Oryx*-like features. If it is indeed *H. gigas*, then it is not very large (Fig. 19) and the tibia and radius are relatively short in comparison with both living *Hippotragus* species. Further comments on hippotragine limb bones can be found in the account of the FLKNN site, in Part II.

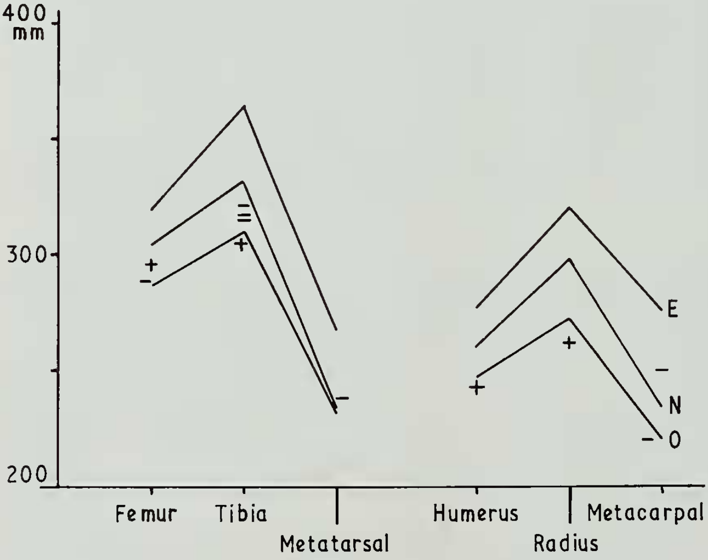

Fig. 19 Lengths of limb bones in Hippotragini. E = mean of 2 *Hippotragus equinus*, N = mean of 4 *H. niger*, O = mean of 3 *Oryx gazella*. Horizontal dashes indicate Hippotragini from Olduvai Bed I, and the crosses show the skeleton FLKNN I 800.

MEASUREMENTS. Measurements on the crania of *H. gigas* are:

	DK I 067/5496 (immature)	FLKNN I 608	VEK I 56 P.P.T.3	Bed II 068/5812
Length of horn core along its front edge	180+	–	*c.* 475·0	*c.* 640·0
Anteroposterior diameter of horn core at its base	47·6	55·3	66·9	87·6
Mediolateral diameter of horn core at its base	42·0	45·6	51·7	73·0
Minimum width across lateral surfaces of horn core pedicels	119·7	137·0	154·0	158·0
Width across lateral edges of supraorbital pits	68·3	–	–	–
Length from back of frontals to top of occiput	87·2	–	89·1	115·5
Length from midfrontal suture at the level of the supraorbital pits to top of occiput	158·0	–	–	213·0
Maximum braincase width	92·0	–	102·0	–
Skull width at mastoids immediately behind external auditory meati	120·0	–	–	148·0
Occipital height from top of foramen magnum to top of occipital crest	–	–	–	68·8
Width of anterior tuberosities of basioccipital	–	42·6	–	–
Width of posterior tuberosities of basioccipital	–	46·6	63·0	54·9
Occlusal length M^1–M^3	–	*c.* 71·2	–	–
Occlusal length M_1–M_3	–	75·8	–	–
Occlusal length M_2	–	24·6	–	–
Occlusal length P_2–P_4	–	42·0	–	–

Anteroposterior and mediolateral diameters at the base of other horn cores of *H. gigas* are:

Bed I BM(NH) M 14530	58·0 × 52·1	GHTK II BM(NH) M 29425	62·0 × 55·8
FLK II 068/6663	57·4 × 49·4	Bed II BM(NH) M 21448	84·9 × 72·5
SHK II 1953.281	63·5 × 52·2	Bed II BM(NH) M 21449	74·9 × 62·2
BK II 1963.3042	77·2 × 64·9	F.3014	83·4 × 75·7
BK II East 1953 P.P.R.5	60·0 × 50·3		

The lengths of FLK II 068/6663 and BK II 1963.3042 are 435·0 and 620·0 mm.

Measurements on mandible FLK I G.067/1097 assigned to *H. gigas* are:

Occlusal length M_1–M_3	78·2
Occlusal length M_2	26·0

An immature mandible SHK II 1957.618 has deciduous P_4 measuring 30·1 mm. An immature maxilla DK I 37+43 has deciduous P^2–P^4 measuring 54·9 mm.

Measurements of length and least thickness on the limb bones assigned to *H. gigas* are:

Femur	DK I 3051	288 × 31·2				
Tibiae	FLKNN I 821	321 × 37·8	FLKN I 1450+1459	317 × 33·6	FLKN I 7207	316 × 41·1
Metatarsal	DK I 200	238 × 26·6				
Metacarpals	FLKNN I 826	236 × 24·3	FLKNN I 960	220 × 26·6	FLKN I 5152	250 × 28·9

Measurements of length and least thickness of the limb bones from the tripartite level of FLKNN I are:

Humerus	800M	243 × 30·7	Tibia	800	305 × 35·2
Radius	800D	*c.* 262 × 34·5	Femur	800A	*c.* 296 × 32·0

COMPARISONS. *Hippotragus gigas* is known at Kanjera by paired horn cores BM(NH) M 15853. An unregistered back of a cranium is probably the same individual, since the register describes M 15853 as 'partial skull and horn cores'. The cranium has a very sloping braincase roof, and a short basioccipital with localized anterior tuberosities situated close together. The proportions of the occipital surface and the degree of development of the temporal lines agree with Olduvai

H. gigas. The anteroposterior and mediolateral diameters at the base of the left horn core are 71·0 × 65·6 mm. A rather small frontlet M 15854 (= *H. equinus* of Hopwood *in* Kent 1942 : 126) and part of a horn core M 25721 could also belong to a *Hippotragus* species. There are three fairly large *Hippotragus* teeth from Kanjera. A left upper molar M 25711 and right upper molar M 25695 are more advanced than any Olduvai *H. gigas*, in their larger basal pillars, complicated central cavities, and ribs localized between the styles. Another right upper molar M 25702 is fairly unworn but probably also advanced in its occlusal pattern. These teeth could well be referred to *H. equinus*.

Two *H. gigas* horn cores come from Peninj, A67.230.1 and A67.230.2 (WN 64.178), and are probably from the same individual. The diameters at the base of A67.230.2, the left one, are 71·9 × 62·2 mm.

The base of a right horn core, Omo 29 69-2646 from member G of the Shungura Formation, Omo, is of *Hippotragus* and has basal diameters of 47·4 × 40·2 mm. Part of a right upper molar, L.17-30a from member C, and perhaps a right lower molar, L.7-g129g from member G, are also hippotragine. The occlusal length of the latter is 24·3 and it is in middle wear. These Omo specimens are probably *H. gigas* or an ancestral species.

What is presumably *H. gigas* is known from the Chiwondo Beds of Mwenirondo, Malawi, by a broken right mandible with part of P_4, M_1, M_2 and part of M_3, BM(NH) M 25305. The occlusal length of M_2 is 29·9 mm. It was recorded as hippotragine by Coryndon (1966 : 66).

There is much well-preserved material from Elandsfontein, including the crania 835, 3211, 15819 and 20975, frontlet 8459, and right horn cores 1919 and 9382E, of a large hippotragine which is apparently conspecific with *H. gigas*. Several hippotragine mandibles (right 1569, 6178, 6179, 15834 and 837B; left 1548, 1634, 2349, 6189, 8362, 8641, 20698, 20983 and others; possibly right 20661 and left 20737) are large and presumably *H. gigas*. They have a larger and longer dentition than the roan, but the premolar rows are actually shorter. The Elandsfontein *H. gigas* horn cores are less compressed and smaller than the largest at Olduvai, though the tooth rows are larger than those from Bed I at Olduvai. The temporal ridges are better developed, the braincase shorter, the occipital low and relatively wider and the median vertical ridge and its flanking hollows possibly stronger in Elandsfontein examples than those at Olduvai. It is possible that *H. gigas* grew to a large size in east Africa in Olduvai upper Bed II times and then declined again later. It would also be possible to regard the Elandsfontein fossils as a separate species, but this has not been done here.

H. gigas is also known from Makapansgat Limeworks, being represented by a right lower molar BPI M.8 and two left upper molars M.34 which were assigned by Wells & Cooke (1956 : 23) to cf. *Oryx gazella*. Parts of horn core bases M.1029 and M.1775, both left, and a damaged frontlet with part of the left horn core M.2795, could be this species.

At Florisbad two right lower molars C.1473 with occlusal lengths of 27·9 and 26·5 mm are within the range for *H. gigas* M_2s based on nineteen Elandsfontein specimens (24·6–32·7 mm). This would be a late record for the species, if confirmed.

Hippotragoides broomi Cooke (1947 : 228, fig. 2) is a hippotragine left mandible from the upper quarry at Sterkfontein (Transvaal Museum No. 835). Apart from the extra basal pillars on the medial side of the molar teeth, which are probably an individual anomaly, the dentition appears from the illustration to agree with *Hippotragus*. It lacks characters of *H. gigas*, and agrees so well with *Hippotragus equinus* that it can be taken as conspecific with the latter. Hopwood & Hollyfield (1954 : 164) included *Hippotragoides* in *Hippotragus*, and Mohr (1967 : 66) thought that *Hippotragoides broomi* was inseparable from *Hippotragus equinus*.

A smaller *Hippotragus* which is very probably the recently extinct *leucophaeus* is known from a number of sites in southern South Africa. The species is represented at Elandsfontein by the basal half of a left horn core SAM 848 and an unnumbered complete right horn core, a left maxilla 2824 + 2826, right mandibles 2833, 3319 and 6323, immature right mandible 1546, left mandible 8261, and some single teeth, at Swartklip by mandibles (Hendey & Hendey 1968 : 54; pl. 5A and B), at Eyre's Cave by a left mandible Q644, at Hawston by a left mandible Q131A and at Bloembos by paired mandibles 661A and B which were called *H. problematicus* by Cooke (1947 : 226, fig. 1). Wells (1967 : 100) has previously suggested that *H. problematicus* is identical with *H. leucophaeus*[2]. Klein (1974a) has established the coexistence of *H. leucophaeus* and *H. equinus* at some Cape Province archaeological sites. This shows that the former was not simply a southern subspecies of the roan, as has been maintained by some zoologists (see Mohr 1967 : 20 for details). *H. leucophaeus* is not known from east Africa.

A *Hippotragus* is represented at Broken Hill, Zambia, by the base of a right horn core BM(NH) M 29484. This is probably the horn core which Leakey (*in* Clark 1959 : 230) identified as *Oryx* sp.

Coppens (1971 : 53) has referred to a *Hippotragus* at Garaet Ichkeul, Tunisia, and Bel Hacel, Algeria, both sites of Villafranchian-equivalent age, but the details are to be published later.

The right horn core but not the teeth of *Praedamalis deturi* Dietrich (1950 : 30; pl. 2, fig. 23) from the Laetolil Beds looks hippotragine. The illustration is an anterior view of what was probably a fairly long horn core when complete. It is nearly straight and shows some compression with anteroposterior and mediolateral basal diameters of 45·5 and 34·1 mm. It is inserted fairly uprightly above the back of the orbit, and the pedicel is hollowed internally. The frontals between the horn core bases are at about the same level as the dorsal parts of the orbital rims. It is interesting that the upright insertion and cross-sectional shape of the horn core resemble *Hippotragus* and its straight course *Oryx*. We shall go on using the generic name *Praedamalis*. Laetolil teeth assigned by Dietrich (1950 : 38, 40; pl. 1, figs 11–12; pl. 3, figs 37–40, 42) to *Aeotragus garussi* and *Hippotragus* sp., and similar teeth in the London and Nairobi collections (Pl. 22, fig. 3), could belong, at first sight, to rather primitive Tragelaphini, Hippotragini or even Boselaphini. The basal pillars and slightly rounded ribs between the styles on the upper molars and the less narrowly pointed lateral lobes and less flattened medial walls of the lower molars could fit primitive tragelaphines. However, the bulbous metaconid of two right P_4s, 1959.456 in Nairobi and M 26777 in London, and possibly the indentations of the central cavities of the upper molars make Hippotragini a more likely identification. We believe that these teeth could be of *Praedamalis deturi*.

A Laetolil horn core from Deturi-Mittellauf was figured as 'Aepycerotinae gen. et sp. indet.' by Dietrich (1950 : 30; pl. 4, fig. 45). It is large and long, only slightly compressed mediolaterally, with transverse ridges, a tendency to flattening of the posterior part of the lateral surface and probably with a posterior keel (damage to the basal part precludes certainty on this). Internal hollowing of the pedicel is unlike that of alcelaphines. Seen anteriorly it has quite a strong basal divergence which lessens distally. This and the very poor backward curvature are not unlike *Beatragus*. The base of a left horn core in Berlin labelled 'cf. *Strepsiceros*, K.L. 2/39' from the Garussi area, and the base of a right labelled 'Tragelaphine, 11/13.1.39' (but given as 11/2.1.39 and 11/12.1.39 on its accompanying card) which definitely has a posterior keel, would both be the same species. The horn core assigned to *Gazella kohllarseni* by Dietrich (1950 : 25; pl. 1, fig. 7) could be a female individual of the same species. We assign all this material to ? Hippotragini sp.

A complete left horn core from Sahabi, Libya, now in Rome, is possibly an early member of the *Hippotragus* lineage. It has preserved part of the orbital rim and frontal. Among its interesting features are strong backward curvature, no flattening of the lateral surface, a small supraorbital pit right at the base of the horn pedicel and incipient frontal sinuses. Its length is 320 mm and its basal index 46·7 × 36·6 mm. The Sahabi fauna has been thought to have an age of about 6 million years (Maglio 1973 : 70).

A fossil hippotragine with a resemblance to *H. gigas* is the holotype cranium of *Sivatragus bohlini* Pilgrim (1939 : 80, text-fig. 6; pl. 2, figs 3–6) from the Pinjor Formation of the Siwaliks. It has a short braincase and a small, short basioccipital with localized anterior tuberosities like *H. gigas*, but it differs in being smaller, having more upright horn core insertions, the braincase little angled on the facial axis and temporal ridges stronger at least immediately behind the horn core bases. These characters are reasonably interpreted as primitive, and the last two would support the idea of a boselaphine ancestry for *Hippotragus*. Other characters shown on the

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[2] Mohr (1967 : 64) stated that *problematicus* agreed well with *equinus*, but also that it differed from *leucophaeus*. This second opinion, based on premolar/molar row proportions, apparently arose from comparison with a skull in the Hunterian Museum of Glasgow University, identified as *H. leucophaeus*. However, Mohr's illustrations suggest that the Glasgow skull could well be a sable, in which case the difference of *problematicus* from *leucophaeus* becomes non-proved.

Siwaliks cranium are the probable internal hollowing of the left horn core pedicel, the braincase widening posteriorly and being low and wide, the occipital surface facing partly laterally as well as directly backwards on each side, the mastoids large, the nuchal crests slightly concave upwards and the auditory bullae probably small. *S. bohlini* can probably be placed in *Hippotragus*. The only other species included in *Sivatragus* is *S. brevicornis* Pilgrim (1939 : 83; pl. 2, figs 7–9) which has still more upright horn core insertions and a more angled braincase. It is possible that it is not hippotragine at all. Pilgrim (1939 : 84–86, text-fig. 7) referred to Tatrot dental remains which are certainly reminiscent of Hippotragini, but it is interesting that on P_4 of the mandible BM(NH) M 15373 there is fusion between the paraconid and metaconid, a feature not found in later, more definite Hippotragini.

Supposed Hippotragini from the Miocene of Samos, Pikermi, Maragha and China are really Caprinae (Gentry 1971), and the tribe is unknown outside Africa, Arabia and India.

The right mandible SAM Mb 1 and deciduous right P_4 Mb 122 from Melkbos recorded as cf. *Hippotragus* sp. (Hendey 1968 : 110) are bovine.

Genus *ORYX* Blainville 1816

Type species. *Oryx gazella* (Linnaeus 1758).

Oryx cf. ***gazella*** (Linnaeus 1758)

1965 *Oryx* sp. indet. Leakey: 51; pl. 62.

One or perhaps two horn cores represent an oryx at Olduvai. An almost complete left horn core with part of the frontal and orbital rim, FLK I G.390 (Leakey 1965 : 51; pl. 62), is definitely *Oryx*. It is inserted slightly closer to the orbit than in living species, but whether the inclination was equally low cannot be determined. Its length along the front edge is 375 mm, and the anteroposterior and mediolateral diameters at its base are 49·0 and 43·5 mm.

A second specimen may well be *Oryx* but the identification is not quite certain. This is BM(NH) M 14532, the lower part of a horn core with part of the pedicel, found in Bed I in 1932. The pedicel has been crushed, and we cannot say whether the horn core is from the right or left side. Its anteroposterior and mediolateral basal diameters are 40·0 and 36·5 mm.

Comparisons. The right mandible BM(NH) M 25304 and probably the immature right one M 25303 from the Chiwondo Beds of Mwenirondo, Malawi, recorded as hippotragine and possibly *Oryx* by Coryndon (1966 : 66) are in our opinion bovine and probably *Syncerus*.

The two left upper molars from Peninj, A67.290 (WN 64.73 MMGN ? USC) and A67.305 (WN 64.209), formerly identified by Gentry (*in* Isaac 1967 : 252) as possibly *Oryx*, are probably alcelaphine, albeit that the second one has a small basal pillar. Oryx teeth are not very markedly specialized in their occlusal pattern, and are therefore likely to be confused with teeth of other antelopes; identifications of oryxes based on teeth alone should be treated with caution.

A small oryx frontlet, Omo 78 69-2731, comes from near the top of member G in the Shungura Formation, Omo, and differs from living oryxes by the slight mediolateral compression, lack of any hint of backward curvature and the rather upright insertion of its horn cores.

Joleaud (1918 : 90, fig. 1) referred a long thin slightly curved horn core from Mansoura near Constantine, Algeria, to *Oryx leucoryx*, believing this to be the specific name applicable to the living west African *O. dammah*. Mansoura is supposed to be of an age equivalent to the Villafranchian, so the horn core is unlikely to belong to a living species despite being very probably an oryx. Coppens (1971) has also referred to an oryx at the Villafranchian-equivalent sites of Garaet Ichkeul, Tunisia, and Ain Hanech, Algeria, but no details are yet published.

A fossil oryx is known by two reasonably well preserved skulls from the Siwaliks. One in Calcutta is *Antilope sivalensis* Lydekker (1878 : 154; pl. 25, figs 1–2), later referred by Lydekker to *Hippotragus* and by Pilgrim (1939 : 77) to a new genus *Sivoryx*. Pilgrim described a second, immature skull in London, 39558, as *S. cautleyi* and made this species the type of the genus. The skulls are probably conspecific, and both were thought by Pilgrim to be of Pinjor age. This fossil oryx differs from the contemporaneous Siwaliks *Hippotragus* in its more angled braincase, absence of temporal ridges on the cranium roof and more obliquely inserted horn cores. Both skulls show very large shallow preorbital fossae which are absent in living oryxes. The London skull shows clearly that the horn core pedicel is hollowed, and that the teeth have basal pillars. The size of the preorbital fossae and the basal pillars are consistent with descent of oryxes from a boselaphine ancestry.

Tribe **ALCELAPHINI**

The Alcelaphini are medium to large, grazing antelopes with long faces, very hypsodont teeth and short premolar rows. They are the commonest antelopes of Olduvai. The group appears to have been in rapid evolution up to the present time but there is a closely similar morphology in many lineages, presumably arising from their adaptations to broadly the same way of life. The main skull features are: skulls long, females horned except in *Aepyceros*, horn core morphology strikingly diverse, horn cores frequently with transverse ridges but generally without keels, often a postcornual fossa which is sometimes shallow and narrow, frontals raised between the horn core bases. Frontals with extensive internal hollowing and a single large sinus extending into the horn core pedicel, braincase short and becoming strongly bent on the facial axis in later forms, temporal ridges wide apart posteriorly, supraorbital pits small, faces generally long and tooth rows set anteriorly, nasals generally long, narrow and without anterior flanges laterally, ethmoidal fissure absent in adults, preorbital fossae still present and often having an upper rim, zygomatic arch usually deepening anteriorly under the orbits, jugal with two broad lobes anteriorly, premaxillae large and rising with nearly even width to a long contact on the nasals, palatine foramina set widely apart, median indentation at back of palate set forward of lateral ones, occipital surface sometimes facing laterally as well as backwards and often with a prominent median vertical ridge, mastoids large, basioccipital with a central longitudinal groove having its sides formed by ridges behind the anterior tuberosities, anterior tuberosities rather wide, foramina ovalia rather large. Upper tooth arcades curved, cheek teeth very hypsodont and with cement, central cavities becoming complicated, medial lobes of upper molars and lateral lobes of lowers rounded, widely outbowed ribs of uppers greatly marked, lower molars without basal pillars or goat folds, short premolar rows, P_2s and sometimes P^2s reduced or absent, P_4s with small hypoconid and with paraconid and metaconid growing together or fused, and mandibles deep under the tooth rows.

The limb bones of Alcelaphini are more distinctive than those of most other antelopes. They show cursorial characters which generally take the form of specializations to improve articulations in the anteroposterior plane, and to allow for strong ligamentous connections around the articular joints. Gentry (1970a : 277–282) discussed cursorial characters in antelope limb bones.

Alcelaphus buselaphus (Pallas 1766), the widespread species of hartebeest, was originally based on the extinct bubal hartebeest of north Africa, but now includes a great variety of named populations, among them the East African *A. b. jacksoni* and *A. b. cokei* as well as the geographically isolated South African *A. b. caama* and *A. b. selbornei*. Fig. 20 shows the great extent of horn core variability within this one species. A high, narrow skull is characteristic of the species, with the horn cores inserted on a high pedicel behind the orbits (or well above the orbits as the head is held in life) and showing rather abrupt alterations in course. The premolar rows are fairly long for an alcelaphine and P_2 is still present.

Alcelaphus lichtensteini (Peters 1849) occurs in grassland areas within the wooded savannah zone from Tanzania to Rhodesia and southern Mozambique. It differs quite markedly from *A. buselaphus* in its wider skull, horn cores inserted widely apart (but still behind the orbits) and longitudinal raising of the midfrontals suture.

Damaliscus lunatus (Burchell 1832) embraces the central African tsessebe (*D. l. lunatus*) and the more northerly races formerly called *D. korrigum*. Like *Alcelaphus buselaphus* the skull is high and narrow, but in this species the horn cores are inserted above the orbits and not on a pedicel, and have a more even curvature with no abrupt changes in course. The horn cores of the tsessebe *D. l. lunatus* are more divergent basally than are those of other races.

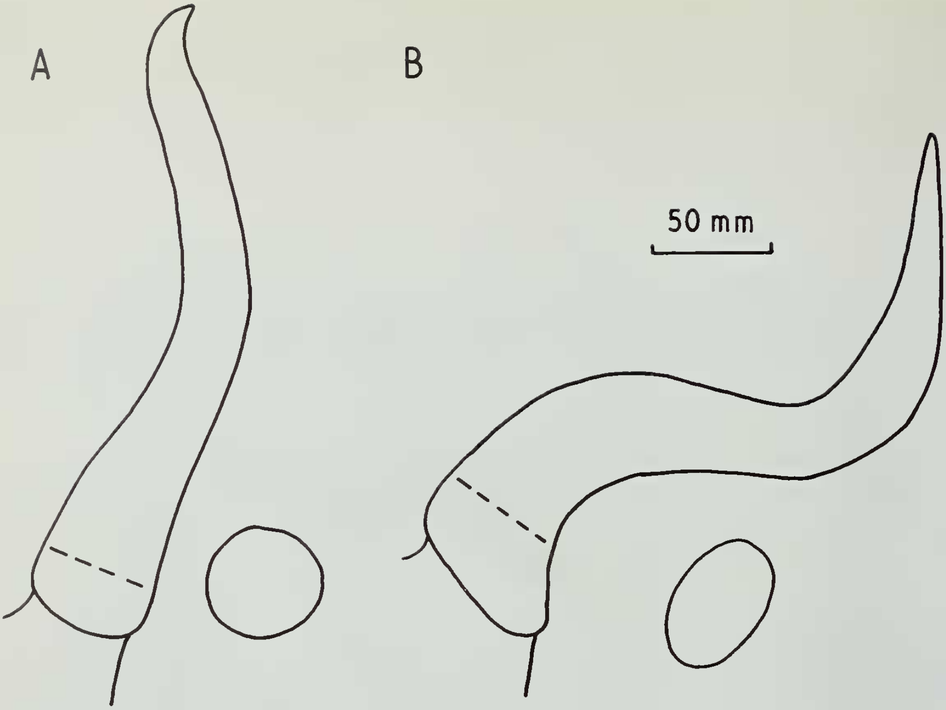

Fig. 20 Infraspecific variation in *Alcelaphus buselaphus* horn cores. A = anterior view and cross-section of left horn core of *A. b. jacksoni*, B = same for *A. b. cokei*. The levels of the cross-sections are marked. The anterior side of the cross-sections is towards the foot of the page.

Damaliscus dorcas (Pallas 1766) is the smaller blesbok and bontebok of South Africa. It differs from *D. lunatus* by having less divergent horn cores, smaller auditory bullae and perhaps more uparched frontals.

Interbreeding between *Alcelaphus* and *Damaliscus* is known to be possible. Selous (1893) referred to a male supposed wild hybrid in Matabeleland (BM(NH) 93.12.17.1). A photograph has been published (*South African Farmer's Weekly*, Bloemfontein, 29 June 1966 : 10) of a hybrid between a male *A. buselaphus selbornei* and a female *D. dorcas phillipsi*. We saw two hybrid skulls (one male, one female) in the Transvaal Museum, Pretoria, apparently the intermediates between *A. buselaphus caama* and *D. dorcas phillipsi* referred to by Kettlitz (1967 : 41). These were such good morphological intermediates that there seems no reason to doubt their origin. Such interbreeding suggests either that the living genera have not been separated for very long or that their gene pools have diverged little since their separation.

Beatragus hunteri (P. L. Sclater 1889), the herola or Tana River hartebeest, has a very restricted range in East Africa. The horn cores are inserted above the orbits and close together, and then diverge outwards. They have long parallel, or sub-parallel, distal parts as in the impala.

Connochaetes gnou (Zimmermann 1780), the black wildebeest of Africa south of the Vaal River, has a wider skull than in *Alcelaphus*, *Damaliscus* or *Beatragus*. The horn cores are inserted well behind the orbits, emerge forwards (downwards with the head vertical), have sharply recurved tips and pronounced basal bosses. The face is shorter than in any other living alcelaphine. The premolar rows are very reduced, and P_2s are missing.

Connochaetes taurinus (Burchell 1823), the blue wildebeest of eastern and southern Africa, has horn cores inserted widely apart and emerging transversely from the skull. The face is longer than in *C. gnou*. This more northern and tropical species is larger than *C. gnou*, just as is *Damaliscus lunatus* in comparison with *D. dorcas*.

C. taurinus has sometimes been generically separated from *C. gnou* as *Gorgon* Gray 1850, and Leakey (1965 : 45) included *Gorgon* in the Bovini. We take *Gorgon* as a synonym of *Connochaetes*, and are happy with the traditional view that it is an alcelaphine (Simpson 1945 : 160; Roberts 1951 : 277; Ellerman, Morrison-Scott & Hayman 1953 : 174). Its skull shows characteristic alcelaphine features: a long face with long narrow nasals, preorbital fossae, the anterior part of the zygomatic arch thickened below the orbits, a bilobed jugal; infraorbital foramen high above the tooth row, a large premaxilla having an even width in side view as it rises to a long contact with the nasals, a central longitudinal groove on the basioccipital and widely set anterior tuberosities, the upper tooth rows well curved with M^3s of opposite sides almost as close as the anterior premolars, very hypsodont cheek teeth, no basal pillars on the molars, rounded medial lobes of upper molars and lateral lobes of lower molars, wide lateral ribs between the styles on the upper molars, lower molars without even incipient goat folds, short premolar rows without P_2s, the P_4 with fusion of paraconid and metaconid giving a continuous medial wall anteriorly, and a deep horizontal ramus of the mandibles.

The limb bones and girdles of *C. taurinus* are very alcelaphine-like in their cursorial proportions and morphology. The *femur* has a fairly deep indentation between the great trochanter and the articular head in anterior view, an anteroposteriorly long lateral part of the articular head and deep pits distally for muscular and ligamentous attachments; the *tibia* has a pronounced tubercle and medial hollow flanking it on the top articular surface, an upcurved edge of the lateral facet and distally a deep central indentation into the rear of the astragalus facet; the *astragalus* has a flange at the top of the medial side visible in anterior view; the *metatarsal* has a greater width across the centre of the top surface than across the rear, lacks a deep hollow between the two naviculocuboid facets and has prominent flanges close together distally on the anterior surface above the condyles; the *scapula* has a large tuber scapulae situated towards the lateral side in ventral view and an unrounded glenoid facet with a posterolateral flattening of its edge; the *humerus* has a wide bicipital groove and a sharp ridge down the front of the lateral tuberosity, a ventral projection at the lateral side of the distal end, distal condyles set uprightly, a small indentation in the top anterior edge of the medial condyle and a well-marked medial groove between the condyles; the *radius* lacks a rim on the medial side of its proximal medial facet, has the back of the lateral facet set well forward of the back of the medial facet, a large and high lateral tubercle, distally the flanges on the anterior surface are strong and close together, and the back of the lunate facet and posteromedial top of the scaphoid facet are well hollowed; and the *metacarpal* has an angled anteromedial corner on its magnum-trapezoid facet and an unciform facet with a small area in relation to that of the magnum-trapezoid facet.

In *C. gnou* some of the alcelaphine-like characters of *C. taurinus* are absent: the long face and nasals, preorbital fossa and anteriorly deepened zygomatic arch. A postcranial skeleton in the South African Museum, Cape Town, failed to show the pronounced tubercle and hollow on top of the tibia, the lack of a deep hollow between the two naviculocuboid facets and the prominent distal flanges on the metatarsal, the small indentation in the medial condyle and the well-marked groove between the condyles of the humerus, and the strong close flanges distally on the radius. Other characters such as the bilobed jugal and the central longitudinal groove on the basioccipital are less pronounced than in *C. taurinus*. However, the unique shape and course of the horn cores of *C. gnou* are not at all like bovines.

Aepyceros melampus (Lichtenstein 1812) is the widespread impala. We classify it as an alcelaphine, but it is undoubtedly well separated from the others.

The Alcelaphini are typically antelopes of open country. Gwynne & Bell (1968 : 390) have shown the connection between the ecological roles of the blue wildebeest and Burchell's zebra on the Serengeti Plains, Tanzania, and a similar relationship could have existed between the black wildebeest and the extinct quagga in South Africa. The extinct north African bubal hartebeest may have lived in rather drier conditions than other hartebeests, perhaps as a result of human persecution. In west Africa *Damaliscus lunatus* ranges further north towards the desert than does *Alcelaphus*, yet in southern Africa *A. buselaphus caama* lives in more arid country than *D. lunatus*.

A number of extinct alcelaphine lineages exist in the fossil faunas, one larger than *Connochaetes taurinus* and at least one smaller than *Damaliscus dorcas*. However, most living and fossil alcelaphines do not differ very much in size. The teeth of Pleistocene fossils show less occlusal complexity, particularly in the folding of the central cavities, than in living species other than perhaps *Connochaetes gnou* and *Damaliscus dorcas*. Because of the rapidity of alcelaphine evolution in the Pleistocene and the late extinction of a number of lineages, it is rather difficult to sort out the stocks.

Genus ***MEGALOTRAGUS*** van Hoepen 1932

1932 *Megalotragus* van Hoepen : 63.
1932 *Pelorocerus* van Hoepen : 65.
1953 *Lunatoceras* Hoffman : 48.
1965 *Xenocephalus* Leakey : 62.

TYPE SPECIES. *Megalotragus priscus* (Broom 1909).

GENERIC DIAGNOSIS. Very large extinct alcelaphines, including the largest known, with narrow skulls and horn cores inserted obliquely in side view, behind the level of the orbits and close together, and with a torsion that is clockwise from the base upwards on the right side; molar teeth tending to have a simple occlusal pattern; very short premolar rows; long legs.

HORIZON. Later levels of the Shungura Formation, Omo, until the end of the Pleistocene.

REMARKS. Our conception is that all the 'giant' alcelaphines of the African Pleistocene can be included in one genus with two species. The species are *Megalotragus priscus*, with long curved horn cores, from South Africa and *Megalotragus kattwinkeli*, an earlier species from east Africa. After Wells (1959 : 124) had considered the species name *priscus* to be a *nomen vanum*, the type cranium of *Bubalis* (=*Alcelaphus*) *priscus* Broom was found in the South African Museum. We were able to see the specimen, SAM 1741, and to confirm its generic attribution to *Megalotragus*. Broom's specific name *priscus* therefore has priority for the South African member of the genus.

Megalotragus kattwinkeli (Schwarz 1932)

1932 *Alcelaphus kattwinkeli* Schwarz : 4, no figure.
1937 *Alcelaphus kattwinkeli* Schwarz : 56; pl. 1, fig. 3.
1965 *Alcelaphus kattwinkeli* Leakey : 60; pl. 78.
1965 *Alcelaphus howardi* Leakey : 60; pl. 79.
1965 *Xenocephalus robustus* Leakey : 62; pls 81–82.
1965 Incertae sedis Leakey: 69 (d) in part.

DIAGNOSIS. Horn cores short to moderately long, inserted behind the orbits but not so far back as to overhang the occipital surface, sometimes dorsoventrally compressed at their bases, with transverse ridges, moderately divergent but much less than in *Connochaetes*, and curved upwards from the base followed by a sharp curve backwards. Median vertical ridge present on occipital, occipital facing primarily backwards and little laterally, basioccipital wide with large anterior tuberosities, auditory bullae small and little inflated.

NEOTYPE. The holotype was a right horn core with frontal, VI-1099 from an unknown horizon at Olduvai, destroyed in Munich in the Second World War. The illustration of this species in Schwarz (1937 : pl. 1, fig. 3) shows a frontal region with horn core bases, which the caption alleges to be VII-468. However, in Schwarz's own list (1937 : 56) of specimens of this species VII-468 is the number of a lower jaw. Further, the skull part shown in pl. 1, fig. 3 does not fit the description of the holotype as a right horn core with frontal. Possibly the figured specimen is in fact VI-487, another listed skull part. Since the original holotype is now lost and was probably never figured, a neotype is now designated: a damaged skull BM(NH) M 21447, previously used and illustrated by Leakey (1965 : 62, pls 81–82) as the holotype of *Xenocephalus robustus* (*International Code of Zoological Nomenclature*, Article 75, Neotypes).

HORIZON. The neotype is from TK (Fish Gully) Beds III–IV at Olduvai, in an area of the Gorge where these beds are not divisible (M. D. Leakey 1971b : 283). It was found in 1931 about 4 feet

1

2

Plate 12 (Scale = 50 mm)

Fig. 1 ***Beatragus antiquus.*** Anterior view of a female right horn core, HWK East II 131.

Fig. 2 ***Megalotragus kattwinkeli.*** Anterior view of left horn core with orbital rim, MNK II 3258.

(1·2 m) below the Masek Beds. The species is known by frontlets and horn cores from middle Bed II to Bed IV, and by apparently conspecific teeth and limb bones from the base of Bed I upwards. It also occurs at Peninj, Chesowanja, the later levels of the Shungura Formation at Omo and possibly in the 'young Pleistocene' of the Laetolil area.

REMARKS. It is not always easy to distinguish isolated horn cores of *Megalotragus kattwinkeli* from *Connochaetes* unless there are cohering parts of the frontals. However, the large size, narrow skull and very long limbs must have contributed to a very different appearance in life from *Connochaetes*, and, with the tendency to an unadvanced occlusal pattern of the molars, must indicate differences in ecology and adaptations.

The neotype skull is rather poorly preserved, and the nasals, premaxillae and right orbital region are missing. Only the left horn core is present, and it shows the characters of dorsoventral flattening at the base and transverse ribbing. There is no sign of a postcornual fossa. The midfrontals suture is complicated, but the frontoparietal suture is not visible. The small supraorbital pits lie behind the level of the orbits, and the infraorbital foramina are above the front edge of P^4. The molars are large with a simple occlusal pattern. The premolar row was probably extremely short as it seems there is room only for the P^4 in front of the M^1–M^3; such a condition may be unique and is certainly unknown in any living alcelaphine. This skull provides a definite horn core–tooth association for the species.

Compared with living *Connochaetes taurinus*, the neotype skull is high rather than low and wide, the braincase is longer, the horn cores are inserted close together and less far behind the orbits, and their course lies more backwards than outwards (i.e. less divergent) and not at all downwards. There is much less of a temporal fossa at the side of the braincase; this is linked no doubt with the closer horn core insertions and with their less extremely posterior position. Compared with a fossil *Connochaetes* cranium and horn cores FLKN I 7154, the neotype is again high rather than low and wide in general shape, the horn cores inserted closer together and their divergence less. There is no doubt that the FLKN I fossil is an early form of wildebeest while, as Leakey (1965 : 62) has pointed out, *M. kattwinkeli* is another line. The horn core of the neotype agrees with the one in Schwarz's illustration in its insertion being close to the mid-line of the skull and somewhat behind the orbits, its degree of divergence and its transverse ridges.

Other cranial remains of *M. kattwinkeli* from Olduvai are: a complete left horn core with a postcornual fossa, part of the frontal and orbital rim MNK II 3258 (Pl. 12, fig. 2); the base of a left horn core BM(NH) M 21484 from the surface of HEK II in 1935 labelled 'cf. *Strepsiceros olduvensis*'; a complete right horn core BK II 1963.3383; the base of a left horn core with the frontal BK II 1963.459; a complete right and possibly female horn core A.72 from JK2 III in 1961 with the frontal, orbital rim and a series of supraorbital pits, and part of the right side of the braincase A.78 preserved separated from the horn core; the basal half of a left horn core with the frontal A.2426 from JK2 III in 1962; the base of a right horn core with the frontal 596 from GC IV referred to by Leakey (1965 : 69) as an unusual member of the Caprinae; a probably female frontlet 068/6664 with complete right horn core and most of the left found *in situ* at GTC IV in 1962 (Pl. 13, fig. 1); and a frontlet with incomplete horn cores F.3013 P.P.F.6 referred to *Alcelaphus* cf. *kattwinkeli*, which was a surface find in 1941 (Leakey 1965 : 60; pl. 78) and has a postcornual fossa and a pit representing the top one of a probable series of supraorbital pits on the left side.

The holotype of *Alcelaphus howardi*, a frontlet with complete left horn core and basal half of the right BM(NH) M 14950 from the surface of SC II in upper Bed II (Leakey 1965 : 60; pl. 79), has horn cores less dorsoventrally compressed at their base than in the neotype but very similar to the slight compression of MNK II 3258. There is no doubt of its identity as *M. kattwinkeli*. The size is right and the horn core about the usual length. The horn cores show transverse ridges in the middle section of the dorsal surface and have moderately strong divergence; above their basal parts they begin to rise and turn inwards and nearer their tips they turn backwards, all as in *M. kattwinkeli*. The left and right sides of the frontlet have been stuck together along their midline, but it is clear that the horn core insertions were close together. The dorsal surface at the base shows rather a broken spongy texture. The base of a right horn core BK II 1963.2718 labelled *Alcelaphus howardi* differs very little from MNK II 3258.

It therefore appears that only one species of large extinct alcelaphine can be identified at Olduvai, and that the correct name for it is *M. kattwinkeli* (Schwarz). There is no reason to place it in a separate genus from the South African species which differs mainly in horn core characters, and in any case *Xenocephalus* is unavailable, being preoccupied by a fish (Kaup 1858) and a beetle (Wasmann 1887); the beetle was later renamed *Wasmannotherium* by Bernhauer (1921).

As Leakey (1965: 60, 63) has noted, *M. kattwinkeli* has certain resemblances to the living *Alcelaphus lichtensteini*. However, the latter has shorter horn cores with insertions wider apart, a temporal fossa, and a longitudinal swelling in the centre of the frontals between the orbits and the horn core bases. The similarities between them are merely fortuitous.

The simple occlusal surfaces of the molars in *Megalotragus* (Pl. 13, fig. 2; Pl. 36, figs 1, 4, 5) show that the influence of allometry is not paramount in alcelaphine teeth. Extant *Alcelaphus*

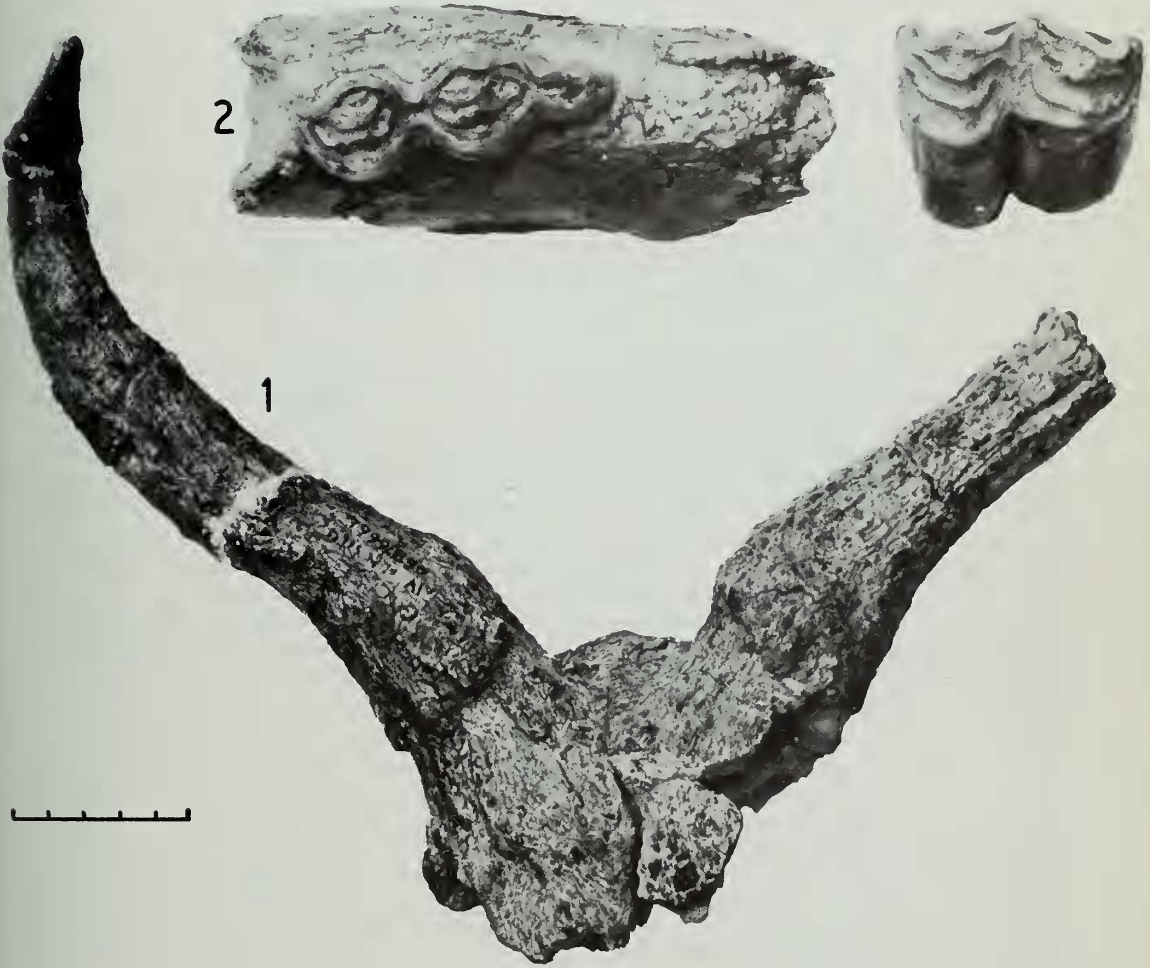

Plate 13 (Scale = 50 mm for the frontlet and 25 mm for the teeth)

Fig. 1 ***Megalotragus kattwinkeli.*** Anterior view of frontlet, GTC IV 1962.068/6664.

Fig. 2 ***Megalotragus* ? *kattwinkeli.*** Occlusal views of teeth: left M_3 DK I 161 (left) and left upper molar DK I 067/3430 (right).

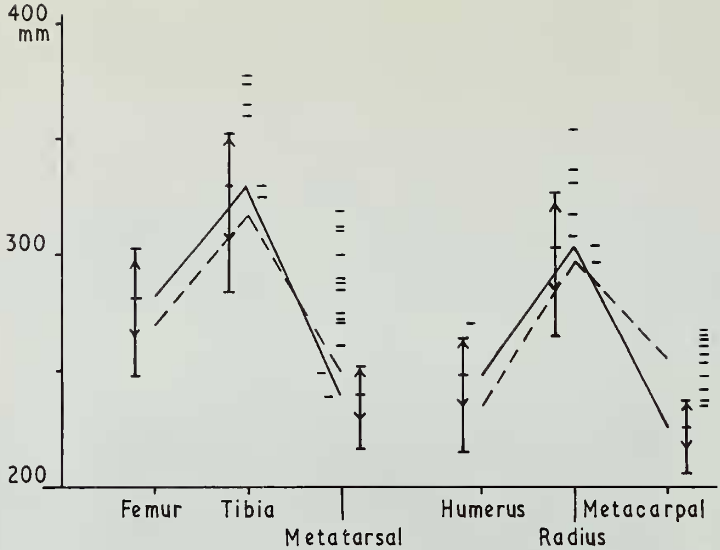

Fig. 21 Lengths of limb bones in *Connochaetes* and *Megalotragus*. Means, ranges and standard deviations are shown for 15 living *C. taurinus*, and the means have been joined up. The dashed line connects the means for *Alcelaphus buselaphus* as a comparison. The metapodials of *C. taurinus* have small ranges and standard deviations. Olduvai fossils are shown as horizontal dashes, the very long bones being of *Megalotragus*.

has fairly complicated occlusal surfaces, and in the larger *Connochaetes taurinus* they are still more complicated, but the very large *Megalotragus* reverses the trend.

Many of the largest alcelaphine limb bones found at Olduvai are too long to fit *Connochaetes* and they almost certainly belong to *Megalotragus* (Fig. 21; Pl. 14). The metacarpal and metatarsal described by Schwarz (1937 : 60, unfigured) as longer than those of *Connochaetes* and assigned by him to *M. kattwinkeli* may have belonged to the latter species, but this is uncertain in the absence of published measurements. However, the left metatarsal VIII-772 assigned by Schwarz (1932 : 4, unfigured) to *M. kattwinkeli* is definitely not long enough for this species, and the radius VIII-345 (Schwarz 1937 : pl. 3, fig. 19) given as *M. kattwinkeli* in the caption but not mentioned in the text is much too small. These limb bones were formerly in Munich but were destroyed in the Second World War.

MEASUREMENTS. Measurements on the more complete specimens of *M. kattwinkeli* are:

	MNK II 3258	JK2 III A.72	TK III–IV M.21447	1941 P.P.F.6 F.3013
Length of horn core along its front edge	280·0	255·0	385·0	–
Anteroposterior diameter of horn core at its base	66·7	48·9	81·9	57·4
Mediolateral diameter of horn core at its base	67·0	48·7	51·5	69·5
Minimum width across lateral surfaces of horn core pedicels	*c.* 130·0	–	129·3	129·6
Width across lateral edges of supraorbital pits	–	*c.* 65·6	*c.* 82·5	–
Maximum braincase width	–	–	107·0	–
Skull width at mastoids immediately behind external auditory meati	–	–	*c.* 175·0	–
Occipital height from top of foramen magnum to top of occipital crest	–	–	67·0	–
Occlusal length M^1–M^3	–	–	92·1	–
Occlusal length M^2	–	–	31·6	–

Anteroposterior and mediolateral diameters at the base of other horn cores of *M. kattwinkeli* are:

SC II surface BM(NH) M 14950	78·1 × 66·8	JK2 III A.2426	54·4 × 49·3
BK II 1963.2718	57·4 × 82·6	GTC IV 068/6664	47·6 × 50·6
BK II 1963.3383	61·3 × 67·3		

The lengths of BK II 1963.3383 and GTC IV 068/6664 are 380·0 and 240·0 mm.

Lengths and least thicknesses of alcelaphine limb bones from Bed I and lower Bed II which could be *Megalotragus kattwinkeli* or its ancestor are as follows. Limb bones and teeth from middle Bed II onwards belonging to size group (i) (see pp. 420–1) include many which are likely to be of *M. kattwinkeli.*

Tibiae	DK I 4300	365 × 35·9	FLKNN I 355	*c.* 377 × 32·0
Metatarsals	DK I 4097	264 × –	HWK East II 2053	319 × 26·4
	DK I 4138	275 × 19·6	HWK East II 067/4691	285 × 24·7
Radii	DK I 166	354 × 37·1	HWK East II 3886	331 × 37·7

Some bones from FLKNN I may be *Megalotragus*, *Connochaetes* or even *Beatragus*. In the account of the FLKNN site we have called them ? *Connochaetes* sp. Their measurements are:

Humerus	358	271 × 34·8	Metacarpal	405	254 × 26·2
Radius	578	304 × *c.* 37·0	Metacarpal	305	235 × 24·1
Metacarpal	577	261 × 27·1			

Radius 578 and metacarpal 577 are associated.

Two large alcelaphine limb bones from FLKN I are:

Metatarsal	8127	312 × 25·2	Radius	181 + 926	297 × 31·0

COMPARISONS. Two Laetolil right upper molars in Berlin referred to *Connochaetes taurinus major* have occlusal lengths of 30·9 (Dietrich 1950 : pl. 2, fig. 18) and 34·6 (pl. 2, figs 19, 20) and therefore are large enough for *Megalotragus*. They come from the 'young Pleistocene' of the Garussi area, not from the old fauna.

M. kattwinkeli is represented at Peninj by left horn core bases A67.228 (WN64.299.2PT3.USC) and A67.234 (WN64.18.CFG III.MZ) and a complete right radius A67.323.1 + A67.345 (WN64. 300A.2PT3.USC). The second horn core was misidentified as *Connochaetes* by Gentry (*in* Isaac 1967 : 253).

M. kattwinkeli is present at Chesowanja in the Baringo district of Kenya (Carney *et al.* 1971 : 509). A young adult right mandible KNM CE 006a + b with P_4–M_3 preserved has occlusal lengths of M_1–M_3 86·7, M_2 29·4 and P_4 17·2. Some single teeth may also be this species.

M. ? *kattwinkeli* is represented in higher levels of the Shungura Formation, Omo by a frontlet with horn core bases F.203-33 and a right horn core F.203-34, both in member K, and by a pair of sub-adult horn cores P.947-1 in member G. These horn cores seem to be 30% or more longer than Olduvai examples, and have a trace of backward curvature at the base. Dorsoventral flattening at the base is poor or absent, and the member G pair are less curved towards the tip. Some of the large alcelaphine teeth in this formation are also likely to be the *Megalotragus* lineage, going back to earlier members.

The large extinct South African *Megalotragus priscus* (Broom) includes *Bubalis helmei* Lyle (1931 : 38), *Megalotragus eucornutus* van Hoepen (1932 : 63), *Pelorocerus helmei* (Lyle) van Hoepen (1932 : 65), *P. mirum* van Hoepen (1947 : 103), *P. elegans* van Hoepen (1947 : 105) and cf. *Megalotragus eucornutus* of Wells (1964a : 88). *P. mirum* and *P. elegans* were placed in a new genus *Lunatoceras* by Hoffman (1953 : 48). Some sinking of names has previously been proposed by Hoffman (1953) and Wells (1959). The species is known by frontlets and horn cores from a good many sites. All the South African specimens are clearly different from *M. kattwinkeli* in their longer horn cores with fairly even curvature, and in the horn core insertions overhanging the occipital surface. They much resemble the horn cores of the bovine *Pelorovis oldowayensis*, but do not reach the size of the largest *P. oldowayensis* and have a stronger upward component of the horn core curvature.

The holotype cranium SAM 1741 of *Megalotragus priscus* (Broom 1909 : 280, 1 text-fig.) comes from the Modder River in the Orange Free State. It is large, and high and narrow rather than low and wide. The remaining base of the left horn core is dorsoventrally very compressed, and the horn cores would have been more divergent than in *M. kattwinkeli*, inserted close together, well behind the orbits and extremely obliquely. The back of the horn core insertions passes above and behind the top of the occipital. The side of the braincase is possibly not hollowed enough to have formed a temporal fossa. The occipital surface is in one plane, facing backwards. There is a median vertical occipital ridge as in *M. kattwinkeli* but it is poorly developed and there are no hollows on either side. The nuchal crests are not very prominent, unlike *M. kattwinkeli*. The basioccipital is wide and has a central longitudinal groove and the anterior tuberosities are probably as wide as the posterior ones.

A good deal of variation occurs in the horn cores of *M. priscus*, notably in the degree of basal divergence. This is weak in specimens from Cornelia, Elandsfontein, Steynspruit and Mahemspan, but strong in those from Florisbad, Mockesdam and Kranskraal and in the holotype cranium. There is a tendency to a flattened medial surface basally in some Elandsfontein horn cores (845 and 851), presumably linked with their poor divergence. The same phenomenon can be seen in some *Alcelaphus buselaphus caama*. It may be that specimens with weak divergence are ontogenetically younger than the others. It may also be true that those with stronger divergence are from later sites, although this conclusion appears to be contradicted by the Mahemspan site. If an evolutionary trend could be detected despite possible ontogenetic effects, then different subspecific names might be justified: *M. p. priscus* (Broom) for those with strongly divergent horn cores and *M. p. eucornutus* van Hoepen for those with little divergence.

It seems to us that none of the South African specimens can be referred to *Alcelaphus* (cf. Wells 1959). The horn cores of '*Pelorocerus helmei*' from Florisbad happen to resemble a huge kongoni hartebeest (*A. buselaphus cokei*) in front view, but in side view (Hoffman 1953 : pl. 1) are considerably different.

The South African *Megalotragus* appears to be later and more advanced than the East African species. It seems unlikely that *M. kattwinkeli*, with its fairly abrupt changes in horn core course and a possible trend towards shortened horn cores, would give rise to *M. priscus*. However, with the evidence of horn core variability in living *A. buselaphus*, there is a possibility that the Olduvai horn cores are a local variation within one widespread and evolving lineage. The horn core insertions of *M. kattwinkeli* are in a primitive, more anterior position than in *M. priscus*, which would be quite compatible with being ancestral to the later species.

There is no clear association of dentitions with *M. priscus*, but many large alcelaphine teeth at South African fossil sites probably belong to this species, as Wells (1964b : 91) has already suggested for the Cornelia and Vaal River material. The tooth material would include the left mandibles C.1584, C.2325 and C.2451 from Mahemspan (Hoffman 1953 : 48) which are complete enough anteriorly to show that there would not have been a P_2 in life, and C.2472 which almost certainly lacked a P_2 in life. Large teeth from the Vaal River gravels and the Wonderwerk Cave assigned to *Pelorocerus broomi* sp. nov., *P. helmei* and cf. *P. helmei* by Cooke (1949), Cooke (1941 : 305, fig. 2) and Wells (1943 : 267) are probably *M. priscus*. Teeth of cf. *P. helmei* from Chelmer, Rhodesia (Wells & Cooke 1955 : 49), and Makapansgat Limeworks (Wells & Cooke 1956 : 25, fig. 12) cannot be safely assigned at species level within *Megalotragus*; this is because teeth from areas to the north of known horn cores of *M. priscus* could be *M. kattwinkeli*, still alive in Olduvai Bed IV times, and because in South Africa no definite horn cores of *M. priscus* are known earlier than Cornelia.

Klein (1972 : 136) has reported teeth from the latest Robberg levels of Nelson Bay Cave, Cape Province, which are the latest known occurrence of *Megalotragus*. They date from 15 000 to 14 000 years BP (Klein, personal communication), shortly before the end of the Pleistocene.

Genus ***CONNOCHAETES*** Lichtenstein 1814

1850 *Gorgon* Gray.
1934 *Pultiphagonides* Hopwood : 549.

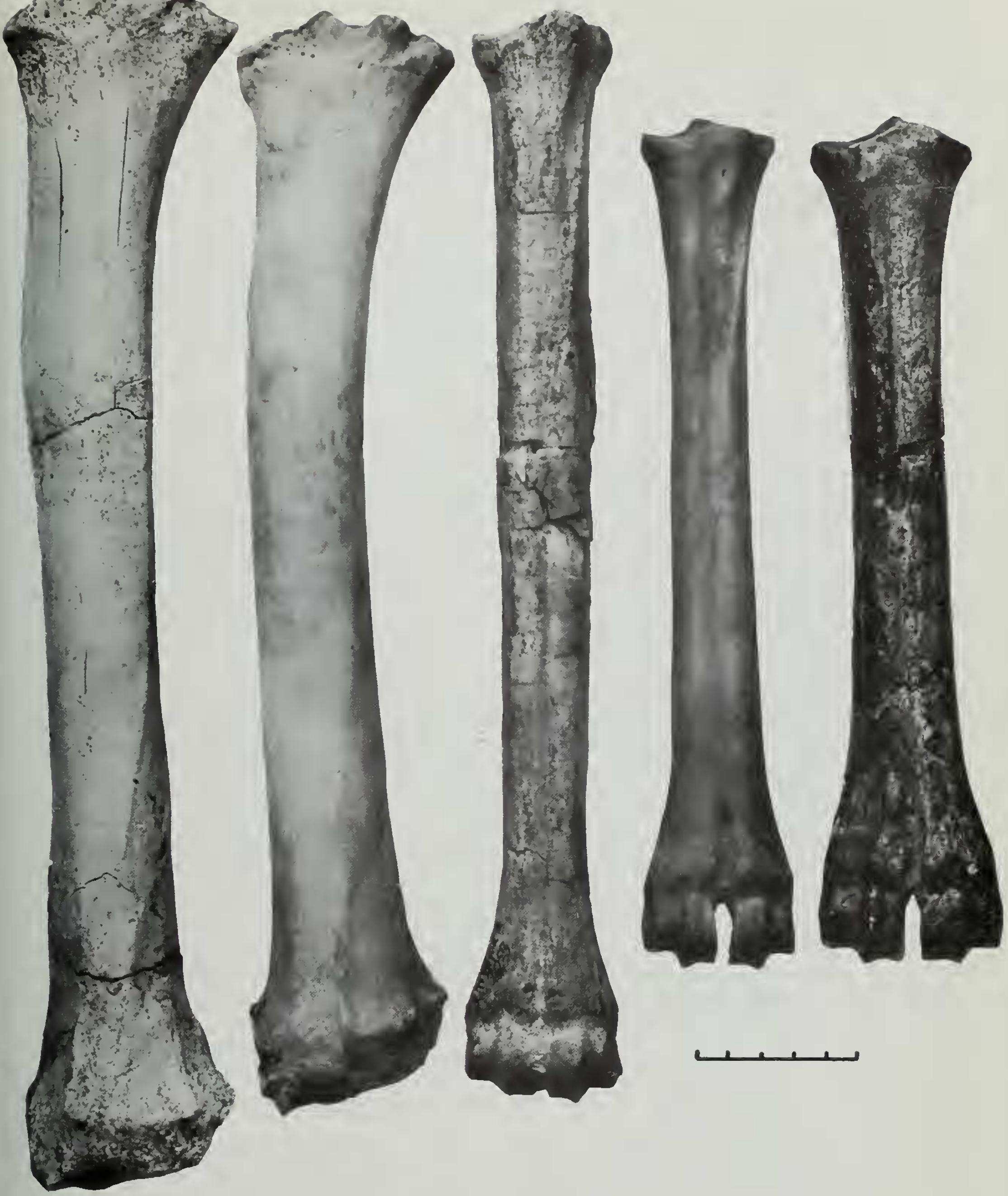

Plate 14 (Scale = 50 mm)

Anterior views of large alcelaphine limb bones. From the left: *Megalotragus* ? *kattwinkeli*, left radius DK I 166; Recent *Connochaetes taurinus*, left radius; *Megalotragus kattwinkeli*, left metatarsal HWK East II 2053; Recent *Connochaetes taurinus*, left metatarsal; ? *Connochaetes*, left metatarsal BK II 1953. 067/5509.

TYPE SPECIES. *Connochaetes gnou* (Zimmermann 1780).

GENERIC DIAGNOSIS. Fairly large alcelaphines with skulls tending to be low and wide; horn cores inserted wide apart and behind the orbits, strongly divergent in earlier species and emerging transversely or forwards in later species. Where torsion exists in the horn cores it is clockwise from the base upwards on the right side. Suture of parietofrontals centrally indented behind horn core insertions; preorbital fossae shallow or absent and without an upper rim; posterior suture of nasals indented centrally; greatest width of nasals usually lying anteriorly; anterior tuberosities of basioccipital more localized than in *Alcelaphus* and *Damaliscus*; auditory bullae large and inflated; occipital surface faces backwards rather than laterally; premolar rows very short with P_2s tending to disappear.

REMARKS. *Connochaetes taurinus* is found as early as middle Bed II at Olduvai, while from Bed I to middle II there existed a more primitive species, here called *Connochaetes* sp. In addition the holotype skull of *Connochaetes africanus* from Bed II appears to belong to the lineage of *C. gnou*.

Connochaetes africanus (Hopwood 1934)

1934 *Pultiphagonides africanus* Hopwood : 549, no figure.
1965 *Pultiphagonides africanus* Hopwood: Leakey : 66; pls 93–94.

DIAGNOSIS. A species of *Connochaetes* in which the horn cores are inserted less posteriorly than in either living species and very widely apart; they pass less downwards and slightly more backwards than in *C. taurinus*. A ridge or traces of one pass across the base of the top surface of the horn core from its anterolateral extremity to its posterior edge. The cranial roof is strongly angled. The face is short and not very deep, the nasals are somewhat widened anteriorly, the zygomatic arch is not thickened anteriorly and a preorbital fossa is absent. A median vertical ridge is still present on the occipital.

HOLOTYPE. Skull with the basal half of the left horn core, right M^1–M^3 and left P^4–M^3, BM(NH) M 14688, found in 1931.

HORIZON. The holotype is from Bed II. We have not assigned any other specimens to this species.

REMARKS. *C. africanus* was not placed in a tribe by Hopwood (1934), but was included in the Caprinae by Hopwood & Hollyfield (1954 : 169), and in the Caprini by Simpson (1945 : 162) and Leakey (1965 : 66). However, in the supraorbital pits and top of the orbital rim being well forward of the horn core pedicel, basioccipital with a central longitudinal groove, much curved upper tooth arcade, shape of the molars' central cavities, and upper molars with rounded medial lobes and wide lateral ribs between the styles, the holotype is clearly alcelaphine. Wells & Cooke (1956 : 26, 33) have already stated that *C. africanus* is alcelaphine on the basis of its teeth, although Cooke & Coryndon (1970 : 214) reverted to placing it as ? Caprinae.

M 14688 is about the size of *C. gnou* and somewhat smaller than other *Connochaetes* from Olduvai. It is definitely adult by the fairly worn left P^4, but the left horn core is rather small. The specimen is probably a female. It is a low and wide skull, the horn core insertions are wide apart with the pedicel carrying the horn core well clear of the skull, and the horn core is somewhat twisted in an anticlockwise direction so that the upper surface comes to face partly backwards at the distal end. The horn core insertions are not so far back as the top of the occipital. The supraorbital pits are wide apart, there is no ethmoidal fissure or preorbital fossa, and the back of M^3 is under the front edge of the orbit.

Apart from its specialized horn cores *Connochaetes gnou* differs from *C. taurinus* at the present time in its shorter face with associated characters of shorter nasals and tooth row set less anteriorly, its less deep face, the zygomatic arch being not deepened anteriorly below the orbits, a less clear preorbital fossa, less pronounced bilobing of the jugals, premaxilla narrower in side view, median vertical ridge still present on occipital, greater reduction of longitudinal ridges on basioccipital, and smaller mastoids. The profile of the nasals and diastemal portion of the maxilla and premaxilla in the two wildebeests suggests that the face of *C. gnou* is less bent down on the postorbital part of the skull, and this would be linked with the absence of a shallow doming of the frontals above the orbits such as is seen in *C. taurinus*. It is interesting that in all these characters which are visible, the *C. africanus* holotype agrees with *C. gnou*: the short and low face, short and anteriorly widened nasals, a more posterior tooth row, an undeepened zygomatic arch, no doming of the frontals and no preorbital fossae. In addition, the very great width between the horn core bases seems almost to be leaving space available for the later development of the enlarged basal bosses of *C. gnou*. This implies that *C. africanus* is ancestral to *C. gnou*, and that this lineage has sometimes occurred in the past to the north of its present range. It may be noted that in mid-wear the molars of present-day *C. taurinus* show greater occlusal complexity than in *C. gnou* (perhaps an allometric effect), but this need not have occurred very far back in the ancestry of *C. taurinus* and therefore is of no help in deciding the affinities of *C. africanus*.

Measurements. Measurements on the skull of *Connochaetes africanus* are:

Width across lateral edges of supraorbital pits	86·7
Height from maxilla edge between P^4 and M^1 to the maxilla–nasal boundary immediately above, at 90° to the tooth row	59·9
Skull width across mastoids immediately behind external auditory meati	135·4
Occlusal length M^1–M^3	63·6
Occlusal length M^2	22·6
Occlusal length P^4	12·0

Comparisons. Material from the Kaiso Formation referred by Cooke & Coryndon (1970 : 214) to *Pultiphagonides* cf. *africanus* does not belong to *Connochaetes*; one horn core has already been mentioned under *Kobus sigmoidalis*, M 12583 and 'M 12558' (= M 12588 ? – AWG) appear to be *Menelikia lyrocera*, while M 26624 is probably alcelaphine but of indeterminate genus. However, the horn core M 12584 does belong to *Connochaetes* (see p. 368).

South African fossils of *Connochaetes* from Cornelia, Elandsfontein and Florisbad can be interpreted as ancestral to living *C. gnou*. The Florisbad *C. antiquus* Broom (1913 : 14, fig. 2) differs from extant *C. gnou* by having horn cores which pass less markedly forwards from the base, and tips perhaps less recurved. At the earlier Elandsfontein site an immediate impression is that the *Connochaetes*, for example the cranium with horn cores 10650, belongs to *C. taurinus* (Wells 1967 : 103), but in fact the base of the horn cores is expanded in dorsal view, and rugose bone has begun to spread across the frontals more than in living or fossil *C. taurinus*. This condition would be appropriate in an ancestor of the black wildebeest. It also occurs in three of the four good *Connochaetes* specimens from Cornelia; these are an unnumbered cranium with complete horn cores, a frontlet C.891 with the base of the left and most of the right horn core, and a partial cranium with left horn core C.892. The fourth specimen, cranium C.622, does not show these features and is much more like *C. taurinus*; it is also the holotype of *Gorgon laticornutus* van Hoepen (1932 : 65, fig. 3). Most probably it is a female. Female horn cores of *C. taurinus* are less anteroposteriorly expanded at the base than males, and the same phenomenon in the Cornelia wildebeest would lead to its females resembling *C. taurinus* males. Horn cores of both the Elandsfontein and Cornelia wildebeests do not pass downwards quite so much, nor are the tips so sharply recurved as in living *C. taurinus*. It is unlucky that nothing is known of the face of the Cornelia fossils to establish beyond doubt that they were on the *C. gnou* lineage. The best classification of this group of wildebeest would be:

Connochaetes gnou gnou the living black wildebeest,
C. gnou antiquus the Florisbad form,
C. gnou ? laticornutus at Elandsfontein,
C. ? gnou laticornutus at Cornelia,
C. africanus from Olduvai Bed II.

Connochaetes sp.

A number of wildebeest fossils from Bed I, lower Bed II and lowermost middle Bed II differ from *C. taurinus* by having horn cores inserted less far behind the orbits, bending less strongly downwards above their base and with tips turned upwards but less inwards. There is no reason to doubt that they are ancestral to *C. taurinus*.

A cranium with complete horn cores and a few isolated teeth, FLKN I 1961.7154 (Pl. 15), was provisionally identified as *Gorgon olduvaiensis* by Leakey (1965 : 46 footnote), but is better designated as *Connochaetes* sp. It is about the size of a female *C. taurinus*, and shows the characters mentioned in the last paragraph. In addition a median vertical ridge was probably present on the occipital.

A horn core cast, HWK EE II 2315, kindly sent to us by Mrs M. D. Leakey in 1972, belongs to *Connochaetes* sp. It is a complete, slender right horn core with much of the frontal, probably from a female animal, and excavated from the Sandy Conglomerate in lower middle Bed II (=level 4 of HWK East II). It has only a short transversely-directed middle section which gives it a markedly primitive appearance. There are transverse ridges on its dorsal surface. We distinguish it from *Megalotragus kattwinkeli* by its long, straight terminal portion, the ridge on its posterior edge near the base, and by the great distance of the insertion from the skull's mid-line as indicated by the incipient temporal fossa. If we are correct in postulating widely separated horn core insertions, then the preserved medial edge of the frontal does not lie along the mid-frontals' suture.

The base of a left horn core with part of the frontal and parietal, BM(NH) M 14518 from Bed I, is of *Connochaetes* sp.

Teeth and limb bones of wildebeest-sized alcelaphines occur at several Bed I sites. They include a left maxilla FLK I B.067/1093 with molars differing from those of the common Bed I alcelaphine *Parmularius altidens* in their greater size and more complicated central cavities. It also has less rounded medial lobes, but this could be a feature resulting from being in early wear; the more worn teeth of FLKN I 7154 have rounded medial lobes. A complete right metacarpal FLKN I 5107 is alcelaphine but not identifiable as *P. altidens* since it is shorter and the distal condyles are too low and wide in anterior view. It could well be of a wildebeest. Some limb bones from FLKNN I have been called ? *Connochaetes* sp., but could easily be of *Megalotragus* or some other large alcelaphine.

MEASUREMENTS. It is difficult to measure anteroposterior and mediolateral diameters at the base of *Connochaetes* horn cores. Those of *Connochaetes* sp. are:

FLKN I 7154 (left)	47·0 × 53·4
HWK EE II 2315 (cast)	46·1 × 54·7
BM(NH) M 14518	56·7 × 58·9

The lengths of the first two are 330·0 and 463·0 mm respectively.

Measurements on dentitions are:

	FLK I B.067/1093 (maxilla)	FLK I B.17 (mandible)	FLKN I 1431 (mandible)
Occlusal length M1–M3	75·5	79·9	76·1
Occlusal length M2	26·7	25·7	23·6

An immature maxilla FLKN I 067/240 has an M^2 measuring 25·8 and deciduous P^2–P^4 at 45·2 mm.

Limb bone measurements of the FLKNN I ? *Connochaetes* sp. have been given on p. 361.

COMPARISONS. *Antilope tournoueri* Thomas (1884 : 15; pl. 7, fig. 1) was founded on a skull top of a primitive wildebeest from Ain Jourdel near Constantine, Algeria. It is of Villafranchian-equivalent age, but from a lower level than the kudu already mentioned from Ain Jourdel (p. 304). Thomas's illustration is a mirror image of the actual specimen. The horn cores are set widely apart and close behind the orbits, they have a circular cross-section and transverse ridges, they curve gently upwards all the way from the base rather than having the upward curvature more localized towards the tips, they diverge strongly but less than in other living or fossil wildebeests, and there is not a noticeable transverse ridge running across the base of the horn core. The primitive characters of insertions so close to the orbits, the consistent and steady upward curvature and the less extreme divergence suggest that the fossil is of greater antiquity than the Olduvai *Connochaetes* sp. A shallow upward doming of the frontals anterior to the horn bases would link it to the *C. taurinus* rather than to the *C. gnou* lineage. Thomas wrongly

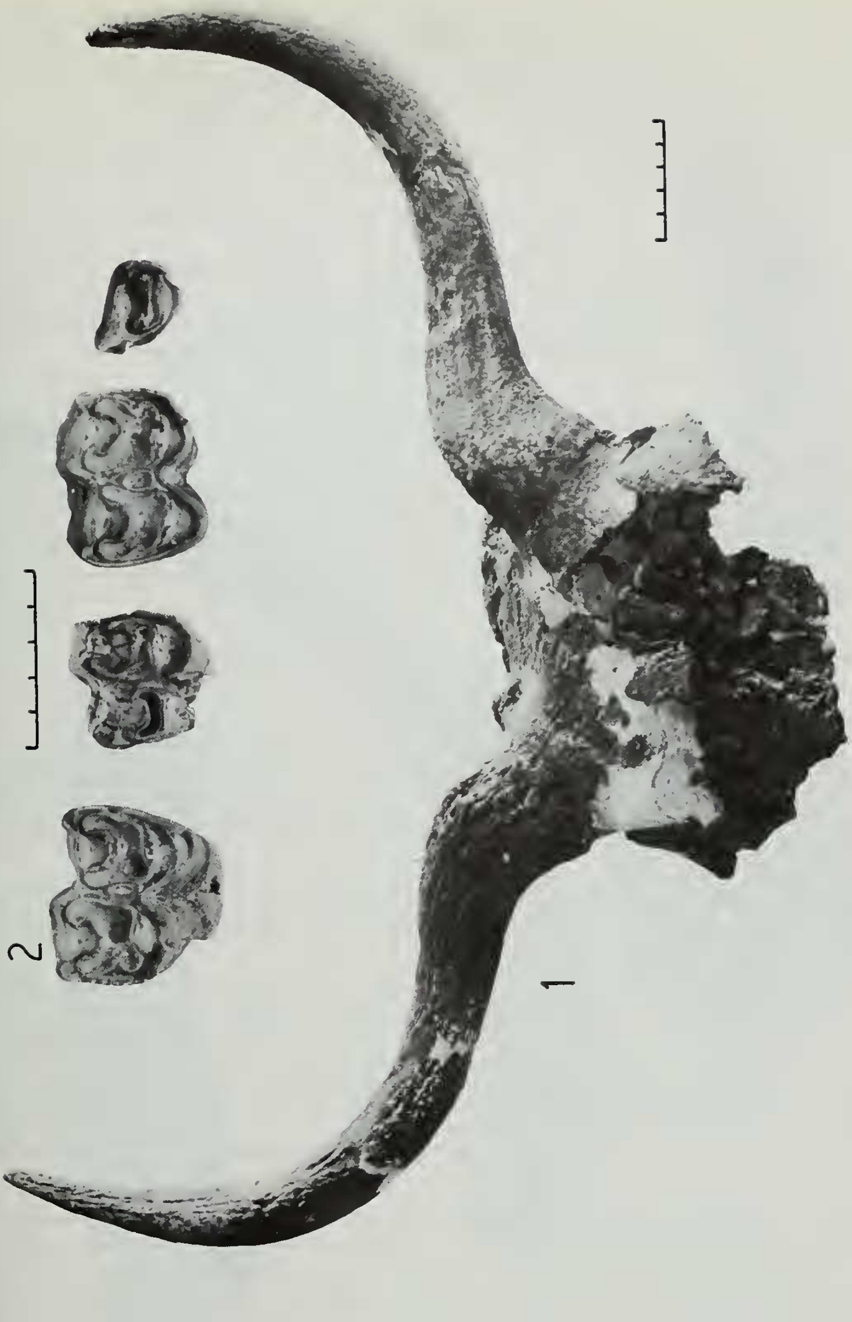

Plate 15 (Scales = 25 mm for teeth and 50 mm for cranium)

Connochaetes sp.; FLKN I 7154

Fig. 1 Anterodorsal view of cranium with horn cores.

Fig. 2 Occlusal views of upper teeth; from the left a right molar, two left molars and a right premolar.

considered that *A. tournoueri* belonged to the Reduncini, and he was followed in this opinion by Pomel (1895 : 45) who founded the generic name *Oreonagor* for it, and by Joleaud (1936 : 1176). Arambourg (1947 : 521) listed it as belonging to *Gorgon*, and the single huge smooth-walled sinus within the right horn pedicel as well as its characters reminiscent of later wildebeest leave no doubt of its alcelaphine status.

The basal half of a right horn core BM(NH) M 12584 from the later faunal assemblage of the Kaiso Formation at Kaiso village belongs to *Connochaetes* or possibly *Oreonagor*[3]. The same identification can probably be made for a horn core L.1-52 from below tuff C of the Shungura Formation.

A complete right horn core, Omo 255 73-5272 from high in member G of the Shungura Formation, belongs to the *Connochaetes* sp. of early Olduvai age rather than to *Oreonagor tournoueri*. It has slight mediolateral compression basally and transverse ridges. Its course is upwards and backwards, then outwards and finally upwards towards the tip.

Connochaetes taurinus (Burchell 1823)

Diagnosis. A larger wildebeest than *C. gnou*; horn cores inserted at the back of the skull above the occipital surface, emerging transversely, having tips turned upwards and inwards, and without a ridge passing across the base of the horn core from its anterolateral extremity; a long face and nasals; zygomatic arch deep anteriorly below the orbits; large shallow preorbital fossa; jugal with two broad anterior lobes; wide premaxillae ascending to a long contact on the nasals; no median vertical ridge on occipital.

Connochaetes taurinus olduvaiensis (L. S. B. Leakey 1965)

1965 *Gorgon olduvaiensis* Leakey : 45; pls 49, 50, 52.

Diagnosis. An extinct subspecies differing from living *C. taurinus* in the horn cores being inserted at a slightly less posterior level and passing less downwards as they emerge from the skull.

Holotype. Top of a cranium with much of its right horn core and base of the left, BM(NH) M 21451 (Leakey 1965 : pls 49, 50).

Horizon. The holotype was found at site VEK at the junction of Beds III and IV. It was found in 1932 according to its label or in 1935 according to Leakey (1965 : 45). Other specimens come from Beds II to IV at Olduvai, Laetolil and Peninj.

Remarks. Other specimens assigned to *C. taurinus olduvaiensis* are a left horn core BK II 1953 P.P.F.1 (Pl. 16, fig. 3; Leakey 1965 : pl. 52 lower picture, which is not BM(NH) M 21452 as stated and is a rear view), and an almost complete right horn core with frontal M 21452 found in Bed IV in 1931 which is the paratype according to the register (Leakey 1965 : pl. 52 top picture which is a dorsal view). A pair of incomplete horn cores 068/6652, together with several pieces of braincase, a right upper molar and an incisor or canine, were found on the surface at MJTK II in 1962 (Leakey 1965 : 105), and may be this subspecies. An incomplete left horn core MNK II

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[3] Since one of us originally informed Cooke & Coryndon (1970 : 214) of the presence of the reduncine *Menelikia lyrocera* in the later fauna at Kaiso, we have looked again for characters whereby its horn cores can be told from those of *Connochaetes*, *Oreonagor* and *Beatragus*.

We found that *Menelikia lyrocera* horn cores from members E and F of the Shungura Formation rise nearly parallel to one another before diverging strongly and bending backwards, hence pieces of sufficient length may show a stronger curve than the alcelaphines. This difference does not exist for many of the *M. lyrocera* from member G and above. Like *Connochaetes* and *Oreonagor* their torsion is clockwise on the right side, so if the side is known *Beatragus* can be eliminated. *Menelikia lyrocera* horn cores taper more rapidly above the base, especially those from member G and above. They have well-marked transverse ridges, which differentiate them from most *Connochaetes*. The sinuses of their frontals rise less far into the horn pedicels and the chambers are smaller than in the alcelaphines.

By these criteria it now appears that the Kaiso horn core BM(NH) M 12584 is of *Connochaetes* or *Oreonagor*. The Kaiso horn cores M 12583, M 12588, M 12589, M 12593 and possibly M 12591 stay as *Menelikia lyrocera*. They resemble horn cores from members E, F and possibly G of the Shungura Formation, Omo, so it is difficult to have them at a time level before member E as suggested by the correlations of Cooke & Coryndon (1970 : 184) and Maglio (1970 : 331; 1973 : 70).

Plate 16 (Scale = 50 mm)

Fig. 1 ***Connochaetes.*** Left horn core, MNK II 2716.

Fig. 2 ***Connochaetes.*** Distal half of a horn core, SHK II 1957.946.

Fig. 3 ***Connochaetes taurinus olduvaiensis.*** Left horn core, BK II 1955 P.P.F.1.

2716 (Pl. 16, fig. 1) is probably a female, and may belong to this subspecies. It would be the earliest Olduvai *C. taurinus*, if it could be definitely distinguished from *Connochaetes* sp. Some other registered pieces in London may belong either to this species, or if the Bed I origin of some of them is to be relied on, to *Connochaetes* sp. These are: M 14522 from Bed I, a tip M 14524 from Bed I, M 14534 from Bed I, M 14548 from Bed II, M 14555 from Bed III, a tip M 14556 from Bed III, M 14559 from Bed III, M 14562 from Bed IV and probably M 14527 from Bed I.

The horn cores of *C. taurinus* no longer show any sign of the ridge passing across the base of the front surface from its anterolateral extremity. The effect is as if the former lateral part of the base had become anterolateral by a twisting of the axis. Such a change would be connected with the increasingly transverse emergence of the horn cores.

Some of the fossils show the beginnings of rugose surfaces over the frontals immediately adjacent to their bases, e.g. BK II 1963.1353. This can also be seen in some living *C. taurinus*. Longer series of complete horn cores might show that the tips were less inwardly recurved in *C. t. olduvaiensis* than in living *C. taurinus*; at present we do not know.

Reck (1935 : 218, fig. 1) described an extremely odd-looking skull fragment from Olduvai as *Rhynotragus semiticus*. It had a strongly-arched or updomed profile of the nasals. Schwarz (1937 : 60, 85) supposed that the fossil had been considerably distorted and was really from a wildebeest. He used the name *semiticus* as a subspecies of *C. taurinus* and assigned a great deal of other Olduvai material collected by Reck to the same subspecies. Assuming that this material was all alcelaphine, we doubt that the dentitions, vertebrae and limb bones could all be safely assigned to *Connochaetes*. (Nine pieces of this Reck collection have survived in London, presumably from a pre-war loan to Schwarz, and all are likely to be alcelaphine, but it is much less certain that they can only represent a wildebeest.) The odd holotype of *R. semiticus* seems unlikely to have been a wildebeest because of the lack of a sharply-outlined temporal fossa between horn core base and orbit and the slope of the braincase just behind the horn core bases.

MEASUREMENTS. Measurements on the holotype cranium BM(NH) M 21451 of *C. t. olduvaiensis* are:

Dorsoventral diameter of horn core at its base	53·9
Anteroposterior diameter of horn core at its base	75·2
Minimum width across lateral surfaces of horn core pedicels	169·0
Length from midfrontal suture at the level of the supraorbital pits to top of occiput	159·0

Anteroposterior and mediolateral diameters at the base of other horn cores of *C. t. olduvaiensis* are:

MJTK II 068/6652	41·4 × 71·8	BK II 1955 P.P.F.1	55·5 × 75·5
MNK II 2716	45·9 × 47·8 (perhaps not this subspecies)	BK II 1963.1353	57·9 × –
		Bed IV BM(NH) M 21452	61·9 × 84·2

The length of BK II 1955 P.P.F.1 is 385·0 mm.

COMPARISONS. Two pieces of one or more right horn cores 1959.44 and 1959.45, and possibly part of a third 1959.337, from Laetolil are of *Connochaetes* and comparable with horn cores from BK II and living *C. taurinus*. They do not derive from the older horizons of Laetolil.

Two pieces of a large skull on which the horn cores have not been preserved, A67.268 (WN64.388 MMG.BSC) from Peninj, belong to *Connochaetes*. The width across the left frontal from the mid-line to the missing horn core base is too great for *Megalotragus*. The anteroposterior level of the horn core insertions agrees well with *C. taurinus olduvaiensis*, the face is longer than in *C. africanus*, and a preorbital fossa of moderate area and extreme shallowness is present. The occipital is rather high, which is probably linked with the anteroposterior level of the horn core insertions. The skull is very large in comparison with the living blue wildebeest. *Connochaetes* is also represented at Peninj by a left horn core base A67.233 (WN64.14 CFG III.MZ), the distal part of a right horn core A67.250 (WN64.142 RDGS.BSC), the middle part of a horn core A67.241 (WN64.238 JHG? USC?), and other horn core, dental and limb bone remains. The distal horn core is about as recurved as in living *C. taurinus*. We identify the Peninj fossils as *C. t. olduvaiensis*.

Arambourg (1938 : 38) assigned a cranium from Témara, Morocco, to *C. taurinus prognu* Pomel, drawing attention to the high occipital and to the short distance between the horn core base and the orbit. His pl. 4, fig. 4 illustrates this last character, and his pl. 3, fig. 3 shows that the horn cores do not pass at all downwards as they emerge from the skull; both these features suggest the strong possibility of subspecific identity between the Moroccan and Olduvai wildebeests. We have not formally sunk *C. t. olduvaiensis* because the original material of *C. t. prognu* described and illustrated by Pomel (1894 : 9; pl. 3, figs 1–4 for horn cores) is insufficient for reliable subspecific determination and because Témara, being of late Pleistocene age, may postdate the east African time range of *C. t. olduvaiensis*. Description of further material of *C. t. prognu* from the type locality (Palikao = Ternifine) may appear in Arambourg's forthcoming monograph. *C. taurinus* survived in north Africa until the late Pleistocene, but Arambourg (1938 : 42) was doubtful about claimed Neolithic occurrences.

C. taurinus is represented at Broken Hill, Zambia, by a number of horn cores, including the left BM(NH) M 12145 and right M 12911 and M 12912. However, some of the horn cores mentioned by Leakey (*in* Clark 1959 : 230) under *Connochaetes* sp. appear to us to be of *Alcelaphus lichtensteini* or its immediate ancestor.

Teeth of *Alcelaphus robustus* from the Vaal River gravels (Cooke 1949 : 20) and of cf. *Alcelaphus robustus* from Makapansgat Limeworks (Wells & Cooke 1956 : 25, fig. 12) may well belong to *Connochaetes*, but of unknown species. The same conclusion should probably also apply to the Chelmer teeth of *Connochaetes grandis* (Cooke & Wells 1951 : 206, fig. 2).

Genus ***PARMULARIUS*** Hopwood 1934

1934 *Parmularius* Hopwood : 550.

TYPE SPECIES. *Parmularius altidens* Hopwood 1934.

GENERIC DIAGNOSIS. Extinct alcelaphines about the size of *Alcelaphus buselaphus*. Horn cores moderate to long, slightly compressed mediolaterally, without keels or torsion, occasionally with transverse ridges in their distal parts, inserted obliquely over the back of or behind the orbits and close together, usually not very divergent but more so distally, and tending to have posteromedial, posterior or posterolateral swellings at the base. Horn core pedicels long (partly connected with the oblique insertions); horns in females; postcornual fossae present; braincase short and strongly angled on the facial axis; a parietal boss placed centrally on the braincase roof; orbital rims moderately projecting; supraorbital pits not set notably wide apart; preorbital fossae small; auditory bullae rather small and not very inflated; premolar rows short; lower molar row sometimes appearing rather small relative to the mandible size.

HORIZON. Beds I–IV at Olduvai. Also found at Peninj, Isimila, Kanjera, the later Shungura Formation at Omo, and possibly Laetolil and Elandsfontein.

REMARKS. Three species of the genus have been named, all with holotypes from Olduvai Gorge: *Parmularius altidens* Hopwood, *P. angusticornis* (Schwarz) and *P. rugosus* L. S. B. Leakey. *Parmularius* probably derives from the same ancestry as *Damaliscus* and *Alcelaphus*, but became more specialized earlier in time. It is not known to have survived the Pleistocene.

Parmularius altidens Hopwood 1934

1934 *Parmularius altidens* Hopwood : 550, no figure.

1965 *Parmularius altidens* Leakey : 56–59, first, second and third additional specimens; further additional specimens (a), (c), (d) and (e), pls 70–74. The horn core FLK I G.230, referred to as a right horn core of *P. altidens* in (b), is in fact the left one of a pair of *Antidorcas recki* horn cores, but possibly the *P. altidens* right horn core 233 is meant. The horn core of pl. 74 is not FLK I F.206 but FLKN I 1410.

1965 Incertae sedis. Leakey : 68(b).

1965 *Okapia* Leakey : 35.

DIAGNOSIS. A species of *Parmularius* about the size of *Alcelaphus buselaphus* or slightly smaller. Horn cores less massive and less divergent in their distal parts than in *P. angusticornis*; earlier populations probably with horn cores strongly and nearly evenly curved backwards, the backward curvature later becoming more distal and finally almost disappearing; horn cores with localized medial or posteromedial swellings at the base. Braincase shortened and strongly angled on the facial axis; large parietal boss on braincase roof; parietofrontals suture indented in front of the parietal boss; each side of the occipital surface facing partly laterally; auditory bulla perhaps larger than in later *Parmularius* species; central cavities of upper molars not quite so curved as in living *Alcelaphus* and *Damaliscus*; premolar rows short; P_2s sometimes absent.

HOLOTYPE. Skull with the basal part of both horn cores, mandibles and cervical vertebrae, BM(NH) M 14689, found in 1931.

HORIZON. The holotype was found in upper Bed I near the mouth of the HWK gully (M. D. Leakey 1971b: 286; personal communication). Other specimens come from Bed I and from member H of the Shungura Formation, Omo.

REMARKS. *P. altidens* is a common alcelaphine at Olduvai. The holotype skull is about the size of a blesbok and is high and narrow rather than low and wide. The horn cores are mediolaterally compressed and inserted behind the orbits. The postcornual fossae are shallow and elongated. The braincase sides are parallel in dorsal view, and the skull-top sutures are not very complicated. The supraorbital pits lie just behind the plane of the middle of the orbits. The zygomatic bar is probably deepened below the orbit; it survives only on the left side and the surface of the bone has disappeared. The back edge of M^3 lies at a level below the front edge of the left orbit; the right orbit is missing apart from some restoration in plaster. The nuchal crests are not very prominent, and each side of the occipital surface probably faced posterolaterally although the central parts have been plastered. The mastoids are large. A number of characters of the face would probably have been found throughout the genus: the small and very shallow preorbital fossae, slight upper rims to the preorbital fossae, infraorbital foramina above the front halves of the P^4s, and the wide premaxillae. The mandibles are large and deep, and both upper and lower

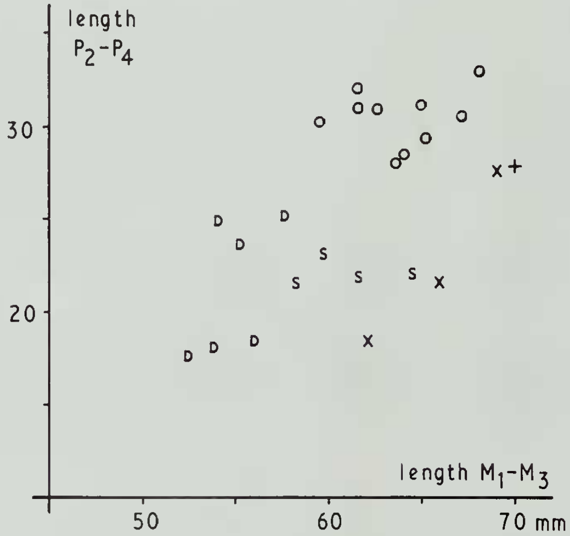

Fig. 22 Lower premolar row/molar row proportions for some alcelaphines. O = East African *Damaliscus lunatus*, D = *D. dorcas*, S = *D. agelaius*, X = *Parmularius altidens*, + = *Damalops palaeindicus* BM(NH) 39571. *Damaliscus agelaius*, having no P_2, has a shorter premolar row than living *Damaliscus* but not as short as the *Parmularius*.

Plate 17 (Scale = 50 mm)

Horn cores of ***Parmularius altidens*** to show the evolution of a straighter profile in Bed I. From the left: medial view of right horn core, DK I 068/6696; lateral view of left horn core of frontlet, FLK I Balk 126+199; lateral view of left horn core, FLKN1 1410 P.P.R.6.

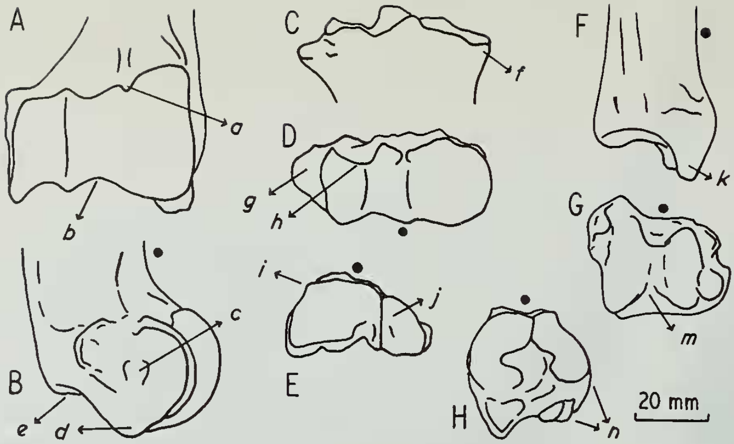

Fig. 23 Limb bones of *Parmularius altidens* from FLKN I to show alcelaphine characters. (Solid dots show anterior sides.)

A. Anterior view of distal right humerus 1961.7070.
B. Lateral view of same distal humerus.
C. Anterior view of proximal right radius 1960.2+57.
D. Proximal articular surface of same right radius.
E. Proximal articular surface of right metacarpal 1962.8836.
F. Medial view of distal left tibia 1961.7074.
G. Distal articular surface of same tibia.
H. Proximal articular surface of right metatarsal 1960.88.

a = indentation at top of medial condyle,
b = deeply incised medial groove,
c = deep hollow for lateral humeroradial ligament,
d = V-shaped ventral edge of lateral side,
e = high level of back part of lateral side distally,
f = no medial rim on top articular surface,
g = large lateral tubercle,
h = back of lateral facet set well forwards,
i = angled magnum-trapezoid facet (less marked than in living alcelaphines),
j = relatively small unciform facet,
k = medial malleolus, less long than in living alcelaphines,
m = deep rear indentation into distal articular surface,
n = articular surface less wide posteriorly than in the centre.

P2s are present. Leakey (1965 : 57) has pointed out that the holotype skull is probably a female, so the females were horned and one may expect horn cores of males to be larger.

Other specimens in London are a complete left horn core BM(NH) M 14514 (Leakey 1965 : 58; pl. 71), the distal part of a horn core M 14515, a frontlet with basal halves of both horn cores M 21455, the base of a right horn core M 14520, and the base of a left horn core M 14528 which were all found in Bed I in 1931. Two incomplete horn cores, M 14540 and M 14550, came from Bed I in 1932, and the base of a right horn core M 29416 from the surface of SC II in 1935. A frontlet with horn core pedicels, M 14529 from Bed I, is also probably *P. altidens*. In Nairobi a horn core F.953 and the base of a left horn core F.1011 were Bed I surface finds in 1941. The horn core FLKN I 637, referred to as an adult giraffid of the okapi type by Leakey (1965 : 35), is in fact a *P. altidens* horn core found in 1960 and has been identified as such by Dr Leakey on its accompanying card. The horn core 1960.749 P.P.R.9 from FLKNN I which was noted as probably Caprini by Leakey (1965 : 68 (b)) is more likely to be the distal half of a *P. altidens* horn core.

The species is most numerous at FLKN near the top of Bed I, but is also represented by seven horn core pieces and other remains at FLK lower in Bed I, and by a single horn core from DK near the base of Bed I. The DK horn core, 068/6696 from the right side, differs from the FLKN ones by being shorter, more backwardly curved, having slight transverse ridges on the upper anterior surface, and by the swelling at the base being smaller and more localized posteromedially (not medially) at the junction of the horn core proper and pedicel. The FLK horn cores show some advance towards those of FLKN in having their backward curvature restricted to the more distal parts of the horn core (Pl. 17). This may be an example of infraspecific evolution of horn cores in the fairly short period during which the Bed I deposits were accumulated at Olduvai. However, other explanations are possible, such as local distributional changes of contemporaneous subspecies, and in any case one would like more than the one horn core from DK.

Plate 18 (Scale = 50 mm)

Anterior views of right limb bones of ***Parmularius altidens*** compared with Recent hartebeest. From the left: ***Alcelaphus buselaphus***, humerus; ***Parmularius altidens***, humerus, FLKN I 7070; ***Alcelaphus buselaphus***, radius; ***Parmularius altidens***, radius, FLKN I 2+57.

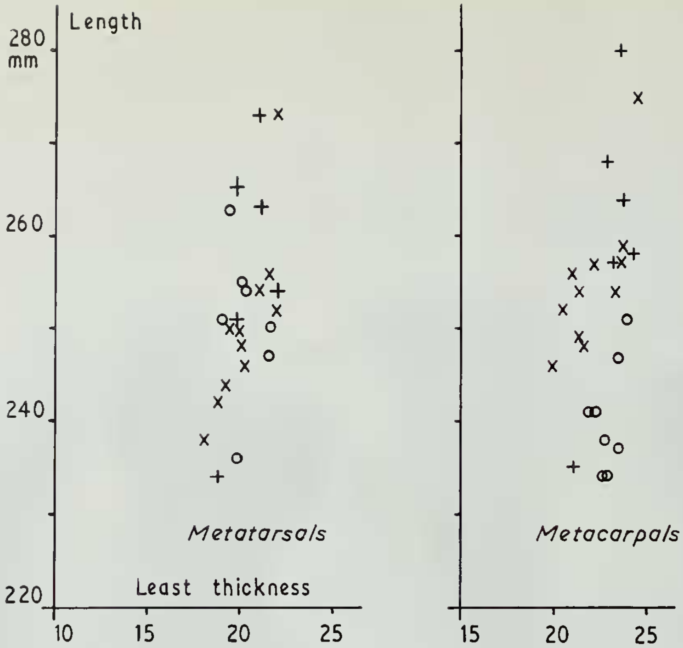

Fig. 24 Metapodial proportions in *Parmularius altidens*.
O = *P. altidens*, X = *Alcelaphus buselaphus*, + = *Damaliscus lunatus*. The metacarpals, but not metatarsals, of *P. altidens* are shorter than in the living alcelaphines.

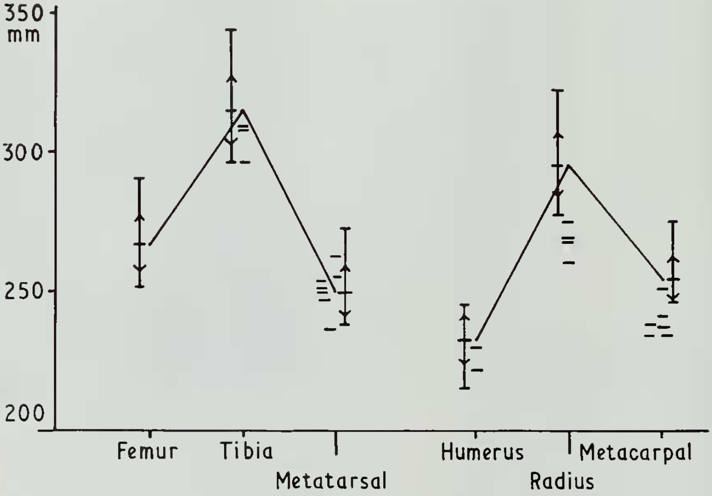

Fig. 25 Lengths of limb bones in *Parmularius altidens* and living *Alcelaphus buselpahus*. Horizontal dashes show individual readings of the right side for *P. altidens*. Means, ranges and standard deviations are shown for 11 *A. buselaphus*, and the means have been joined up. *Damaliscus lunatus*, not shown here, has proportions very like *A. buselaphus*.

Plate 19 (Scale = 50 mm)

Fig. 1 Limb bones of ***Parmularius altidens*** compared with those of Recent hartebeest in anterior view. From the left: ***Alcelaphus buselaphus***, right metatarsal; ***Parmularius altidens***, right metatarsal, FLKN I 88; ***Alcelaphus buselaphus***, right metacarpal; ***Parmularius altidens***, right metacarpal, FLKN I 8836.

Fig. 2 Short metapodials of ? **Caprinae** sp. from FLKN I. From bottom upwards: left metacarpal, 9394; left metatarsal, 068/6665; right metatarsal, 067/1009.

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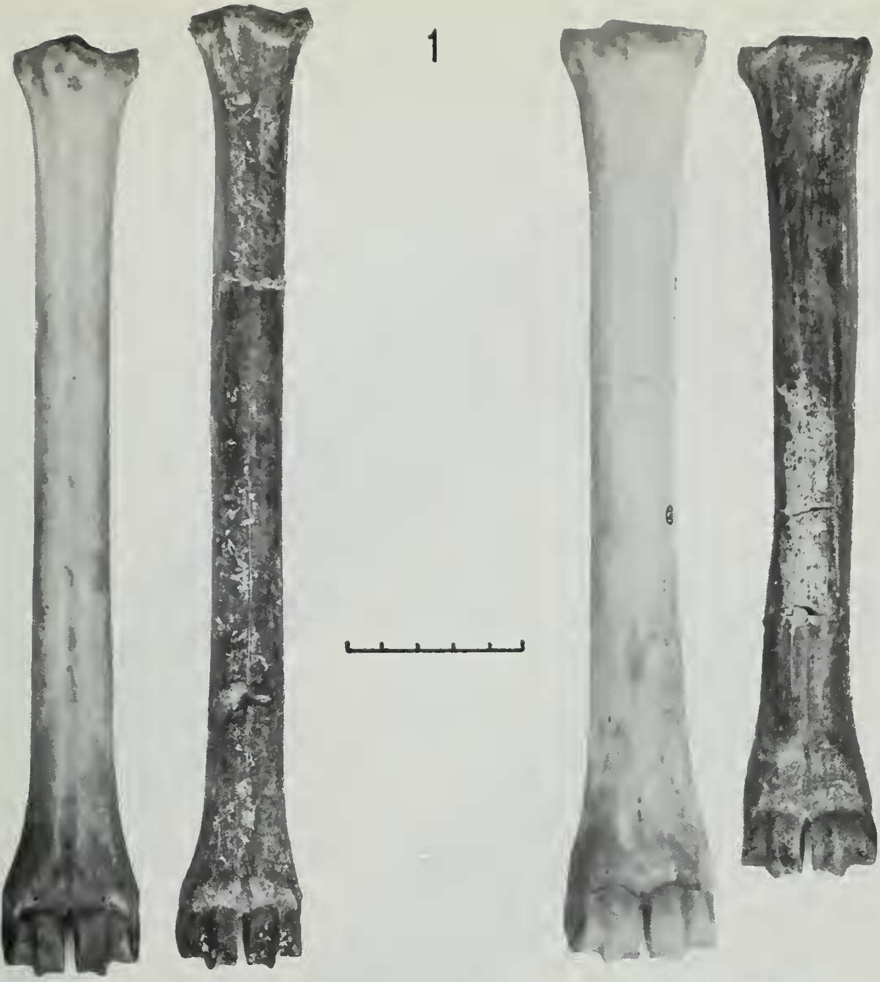

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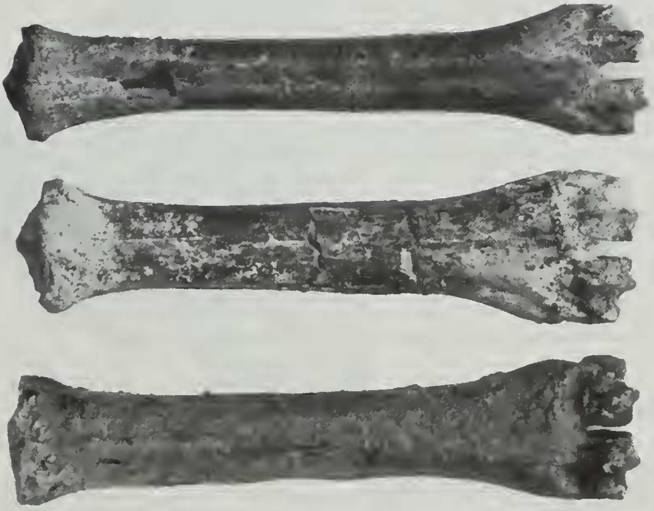


The dentitions of *P. altidens* (Pl. 30, fig. 2; Pl. 37, fig. 5) are slightly smaller than in the living hartebeest. The teeth are like those of living *Alcelaphus* and *Damaliscus* in the rounded medial lobes of the uppers and lateral lobes of the lowers, and in the prominence of the ribs on the lateral walls of the uppers. On the whole, however, the central cavities of the upper molars are not quite so recurved laterally as in living *Alcelaphus* and *Damaliscus*, and the outline of the central cavities of the upper and lower molars is less complicated, though individual teeth cannot always be distinguished from *Alcelaphus* or *Damaliscus*. *P. altidens* in Bed I already has a shorter premolar row than in the Beds III–IV herd of *Damaliscus agelaius* (Fig. 22); often the molar row of *D. agelaius* is absolutely shorter, as well as relatively, than in *P. altidens*. The short premolar rows of *P. altidens* were noted by Pilgrim (1939 : 70). On *P. altidens* mandibles FLK I D.42, FLK I E.129 and FLKN I 1109 there is no alveolus in the jaw for a P_2 so that P_2 was missing in life, but on FLK I G.361, FLKN I 38, FLKN I 208, FLKN I 1198 (right) and probably FLKN I 1728 P_2 or its alveolus is still present.

The many limb bones of *P. altidens* at FLKN I show some differences from those of living *Alcelaphus buselaphus* and *Damaliscus lunatus*. The tibiae have a shorter medial malleolus at the distal end than in most individuals of the living species, and on the metacarpals there is less of an anteromedial sharply angled corner on the magnum–trapezoid facet proximally (Fig. 23). The tibiae and humeri may be shorter than in *A. buselaphus* or *D. lunatus*, the radii and metacarpals are definitely shorter and more robust, but the metatarsals are as long (Figs 24, 25; Pls 18; 19 fig. 1). Thus *P. altidens* would not have been so high at the shoulders as living alcelaphines.

MEASUREMENTS. Measurements on the skull BM(NH) M 14689 of *P. altidens* are:

Skull length from front of the premaxillae to back of the occipital condyles	*c.* 337
Anteroposterior diameter of horn core at its base	30·9
Mediolateral diameter of horn core at its base	27·4
Minimum width across lateral surfaces of horn core pedicels	72·2
Width across lateral edges of supraorbital pits	*c.* 55·6
Height from the maxilla edge between P^4 and M^1 to the maxilla–nasal boundary immediately above at 90° to the tooth row	61·3
Maximum braincase width	83·5
Skull width across mastoids immediately behind external auditory meati	108·7
Distance from rearmost point of occlusal surface of M^3 to back of occipital condyles	139·3
Occlusal length M^1–M^3	64·8
Occlusal length M^2	*c.* 23·2
Occlusal length P^2–P^4	28·3
Occlusal length M_1–M_3	69·1
Occlusal length P_2–P_4	27·7

Measurements on frontlet FLK I Balk 126 + 199 of *P. altidens* are:

Length of horn core along its front edge	330·0
Anteroposterior diameter of horn core at its base	48·8
Mediolateral diameter of horn core at its base	40·6
Minimum width across lateral surfaces of horn core pedicels	95·0

Measurements on seven frontlets and seven horn cores of *P. altidens* from FLKN I are:

	Number measured	Mean	Range	Standard deviation	Standard error
Length of horn core along its front edge	5	263·6	247·0–292·0	–	–
Anteroposterior diameter of horn core at its base	14 (left + right)	42·3	33·3– 50·3	4·3	1·14
	10 (left only)	42·3	33·3– 49·4	4·5	1·44
Mediolateral diameter of horn core at its base	14 (left + right)	36·7	30·8– 44·5	3·8	1·01
	10 (left only)	37·6	30·8– 41·6	4·1	1·29
Minimum width across lateral surfaces of horn core pedicels	4	88·6	79·4– 96·7	–	–

Plate 20 (Scale = 50 mm)

Fig. 1 ***Parmularius altidens.*** Lateral view of partial cranium with horn cores, HWK 1 1962.068/6650.

Fig. 2 ***Damaliscus niro.*** Lateral view of right horn core, SHK II 1953.282.

Anteroposterior and mediolateral diameters at the base of other horn cores of *P. altidens* are:

DK I 068/6696	46·7 × 39·8	HWK I 1962.068/6650	46·6 × 40·0
FLKNN I surface 067/1173	37·5 × 32·3	Bed I BM(NH) M 14514	41·4 × 36·7
FLK I F.206 P.P.F.7	44·2 × 37·9	Bed I BM(NH) M 14520	45·9 × 39·2
FLK I G.232	40·4 × 34·1	Bed I BM(NH) M 14528	39·6 × 41·3
FLK I G.233+235 P.P.R.3	42·7 × 39·8	Bed I BM(NH) M 14540	42·4 × 38·0
FLK I C.067/1078	40·2 × 34·3	Bed I BM(NH) M 14550	42·4 × 38·3
FLK I G.067/1080	41·8 × 36·7	Bed II surface BM(NH) M 29416	47·1 × 44·1

The lengths of DK I 068/6696, FLKNN I surface 067/1173 and FLK I G.233+235 are 260·0, 235·0 and 305·0 mm.

Measurements on maxillae assigned to *P. altidens* are:

	FLKN I 1136	FLKN I 1604	FLKN I 10209
Occlusal length M^1–M^3	60·5	63·5	59·7
Occlusal length M^2	22·6	22·1	21·9

An immature maxilla FLKN I 430 has deciduous P^2–P^4 measuring 40·8 mm.

Measurements on 10 mandibles assigned to *P. altidens* from FLKN I are:

	Number measured	Mean	Range	Standard deviation	Standard error
Occlusal length M_1–M_3	10 (left+right)	64·6	59·4–76·1	5·2	1·65
	6 (left only)	65·2	61·5–76·1	5·6	2·27
Occlusal length M_2	10 (left+right)	20·6	18·7–23·6	1·5	0·48
	6 (left only)	20·7	19·7–23·6	1·5	0·60
Occlusal length P_3–P_4	1	18·4	–	–	–

Measurements on other mandibles assigned to *P. altidens* are:

	FLK I D.42	FLK I G.361	FLK I D.067/1094	FLK I G.067/1098
Occlusal length M_1–M_3	66·0	65·5	60·7	65·6
Occlusal length M_2	20·6	21·1	19·1	20·8
Occlusal length P_3–P_4	21·5	–	–	–

The M_2 on mandible FLKNN I 733 measures 23·0. Immature mandible FLKN I 10212 has deciduous P_4 measuring 23·4 mm.

Measurements on 14 metatarsals assigned to *P. altidens* from FLKN I are:

	Number measured	Mean	Range	Standard deviation	Standard error
Length	14 (left+right)	253	236–270	8·6	2·31
	7 (left only)	255	245–270	9·1	3·43
Least thickness	14 (left+right)	19·5	17·0–21·5	1·3	0·34
	7 (left only)	18·9	17·0–20·9	1·3	0·50

Measurements on 15 metacarpals assigned to *P. altidens* from FLKN I are:

	Number measured	Mean	Range	Standard deviation	Standard error
Length	15 (left+right)	241	234–251	5·6	1·46
	8 (left only)	242	234–249	5·0	1·76
Least thickness	15 (left+right)	22·4	20·4–24·0	1·1	0·28
	8 (left only)	21·8	20·4–23·2	1·1	0·33

Measurements of length and least thickness on other limb bones assigned to *P. altidens* are:

Tibiae	FLK I F.138+141	309 × 26·7	FLKN I 7074	308 × 26·8	FLKN I 7084	296 × 24·2
Humeri	FLKN I 7070	230 × 27·7	FKLN I 067/515	210 × 26·3		

Plate 21 (Scale = 50 mm)

Fig. 1 ? ***Parmularius*** sp. Lateral view of cranium from Laetolil, 1959.277.

Fig. 2 Anterior view of same.

Radii	FLKN I 2+57	269×27·1	FLKN I 688	260×26·7	FLKN I 1046	266×28·4
	FLKN I 7779+7780	266×27·7	FLKN I 8247	283×–	FLKN I 067/4741	268×28·3
Metacarpal	DK I 76	236×24·7				

An associated set of limb bones from DK I, humerus 141 222×26·2, radius 58 275×26·2 and metacarpal 143 241×22·0 mm.

Comparisons. The lower half of a left horn core F.161-37 found in 1972 represents *P. altidens* in member H of the Shungura Formation at Omo.

A well-preserved cranium 1959.277 with most features intact, but damage like that caused by *Ceratophaga vastella* on the front of its horn cores from Laetolil (Pls 21; 22, fig. 2), may be ancestral to *Parmularius altidens*. That it is an alcelaphine is shown by the small supraorbital pits, a low parietal boss, high level of frontals between the horn core bases and a central longitudinal groove on the basioccipital. It could well be primitive in the rather long and little-angled braincase, the close supraorbital pits with a concave surface of the frontals in between them instead of a convex one, and the straight parietofrontals suture behind the horn core bases.

All the characters so far mentioned could be expected in an ancestor of *P. altidens*, although the low parietal boss and the primitive characters bar it from admission to that species. It is additionally different from *P. altidens* in having more uprightly inserted horn cores and localized posterolateral swellings at the base of the horn cores. It does have an occipital surface with strong laterally-facing components which is like *P. altidens*, and might also be primitive. The horn cores curve back fairly abruptly just over half way from base to tip, and there is some similarity between them and the *P. altidens* horn core 068/6696 from DK I.

Measurements on this Laetolil cranium are:

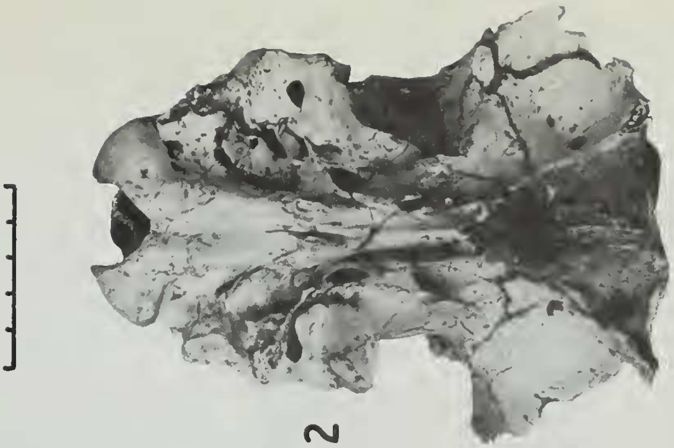
Length of horn core along its front edge	208·0
Anteroposterior diameter of horn core at its base	43·8
Mediolateral diameter of horn core at its base	38·2
Minimum width across lateral surfaces of horn core pedicels	92·8
Width across lateral edges of supraorbital pits	45·7
Length from back of frontals to top of occiput	62·3
Maximum braincase width	73·8
Skull width across mastoids immediately behind external auditory meati	94·3
Occipital height from top of foramen magnum to top of occipital crest	38·0
Width of anterior tuberosities of basioccipital	21·0
Width of posterior tuberosities of basioccipital	28·1

The right horn core from Laetolil which Dietrich (1950: 36; pl. 2, fig. 21) called 'Reduncini gen. et sp. indet.' could be conspecific with the cranium 1959.277. Its basal diameters are 38·8×*c.* 30·3 mm.

Parmularius angusticornis (Schwarz 1937)

1937 *Damaliscus angusticornis* Schwarz: 55, no figure.
1965 *Damaliscus angusticornis* Leakey: 51; pls 63–66.
1965 *Damaliscus antiquus* Leakey: 55; pls 67–69.
1965 *Parmularius* sp. indet. Leakey: 60; pl. 77.
1965 cf. Alcelaphini Leakey: 66(b); pl. 91.

Diagnosis. A species of *Parmularius* about the size of *Alcelaphus buselaphus* or slightly larger; horn cores more massive, with thicker bases and often more divergent in their distal parts than in *P. altidens*; most horn cores almost without backward curvature. Braincase more extremely shortened and more strongly angled on the facial axis than in *P. altidens*; parietal boss less marked than in *P. altidens*; suture of parietofrontals without a central indentation; large occipital surface retaining its median vertical ridge but facing backwards more clearly than in *P. altidens* or *rugosus*; auditory bullae small and little inflated; basisphenoid strongly bent upwards on plane of basioccipital.



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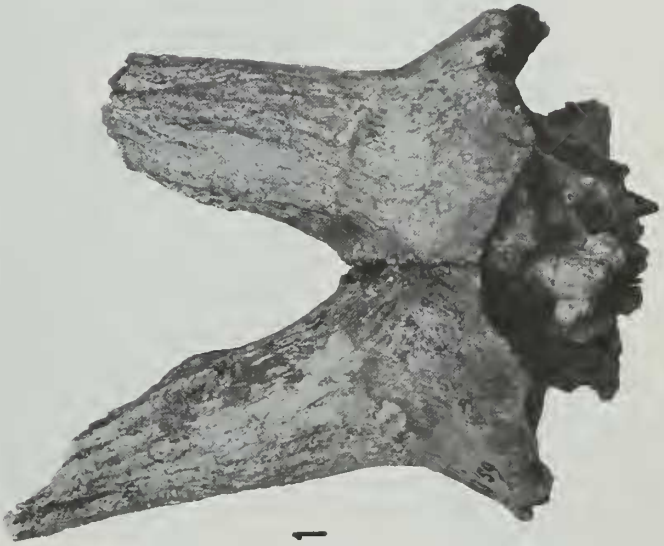

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Plate 22 (Scale = 50 mm for cranial pieces and 25 mm for teeth)

Laetolil fossils

Fig. 1 **Alcelaphini** sp. indet. Anterior view of frontlet, 1959.233.

Fig. 2 ? ***Parmularius*** sp. Ventral view of cranium, 1959.277.

Fig. 3 ? **Hippotragini.** Occlusal view of teeth. From the left: left upper molar 1959.454, right upper molar 1959.453, part of left mandible 1959.56, right P_4 1959.456.

PARATYPE. The holotype was a crushed cranium formerly in Munich but unfortunately destroyed during the Second World War. However, Schwarz had nominated as paratype a partial frontlet with incomplete right horn core in London, BM(NH) M 14553, and this still exists. It was figured by Leakey (1965 : pl. 63).

HORIZON. The paratype is from the surface of Bed II, Olduvai. Other specimens are frequent in middle and upper Bed II. The species is also known from Peninj, Isimila and Kanjera.

REMARKS. This is the largest and morphologically the most advanced species of its genus. It is known only by horn cores and crania. Leakey (1965 : 51) drew attention to the deficiencies of Schwarz's original definition, revised it and figured the paratype. He also described and figured other conspecific specimens: a cranium M 21425 (pls 64–65) found in 1935 *in situ* at SHK II, a frontlet M 21422 (pl. 66) from the surface at VEM in 1935 and a frontlet M 21423 from the surface of SHK II in 1935.

Leakey (1965 : 55) also founded an allied species which he called *Damaliscus antiquus*. The holotype cranium (numbered and catalogued P.P.T.1, not P.P.T.3 as given by Leakey 1965 : 55, pl. 67) was excavated from BK II in 1955, but the paratype cranium BM(NH) M 21428 was found being eroded out at VEK in 1935 and taken to be of Bed I age. However, 'VEK II' is written on the back of the left horn core, while the inscription 'VEK I' on the side of the braincase seems to have been added more recently, perhaps at the time of registration. It is this record which was thought to establish the species as older than *angusticornis*, so that *antiquus* was a fitting trivial name. Three further specimens in Nairobi were a left horn core from SHK II *in situ* 1957.1284, and the base of a left horn core F.963 P.P.R.4 and the basal half of a right horn core with mid-frontal suture and orbital rim F.948, both found on the surface in 1941. *D. antiquus* was said to differ from *D. angusticornis* in the horn cores being inclined slightly backward from the forehead, curving slightly outwards and backwards and then forwards, not tapering so rapidly, without such an abrupt change in cross-section, and sometimes having traces of cross ribbing. The alcelaphine groove (postcornual fossa) of *antiquus* appeared shallower and less well-defined, but with a sharp anterior edge, and the flat-topped protuberance in the centre of the parietals was stronger. The skulls appeared generally larger and more rugose.

The curving of the horn cores slightly outwards and backwards and then forwards is well shown on the paratype of *D. antiquus* (Leakey 1965 : pls 68, 69) but not on the holotype (pl. 67), and this condition is also approached by the *angusticornis* paratype (pl. 63). The larger size and greater rugosity is less true of the *antiquus* paratype than of the holotype. It is also apparent that the assignment of some horn cores excavated from BK II since 1960 is a matter of difficulty; they are without rapid tapering above the base, just as in *antiquus*, but are straight as in *angusticornis*, and while two of them (1963.2499 and 1963.067/1650) have cross ribbing, the other two (1963.3178 and BK II East 1961.068/6660) have not. Other Olduvai pieces are also difficult to place. A damaged frontlet 1962.068/6648 from Long K East, middle Bed II, agrees with *angusticornis* in the abrupt and sudden tapering of its horn cores shortly above the base, but with *antiquus* in their slight inclination backwards and in having a flat-topped parietal protuberance. A cranium BM(NH) M 21429 found at VEK ? II in 1932 (Leakey 1965 : 66(b); pl. 91) resembles *antiquus* in the absence of a marked basal swelling, but the horn cores are straighter than *antiquus* is said to have. A left horn core 1960.068/6126 from the surface of HWK II is larger than the *antiquus* holotype but agrees with *angusticornis* in its pronounced basal swelling, although the postcornual groove is shallow.

It seems then that the two species cannot be distinguished on the wider range of specimens now available, and the prior name is *angusticornis*. We place this single species in *Parmularius* instead of *Damaliscus* because of the thickened bases of its horn cores, the lack of a markedly wide separation of the supraorbital pits, its parietal boss and the very short and strongly inclined cranial roof. All the Olduvai specimens of known horizon are from middle and upper Bed II with the doubtful exception of M 21428. Two crania in Nairobi from unknown horizons are the surface finds F.3015 and 068/5854. Bed II surface finds in 1941 are the left horn core bases F.973, F.3005 and 068/5927, right horn core bases F.948, F.975, F.3005 and 068/5926, and a frontlet with the basal halves of both horn cores F.989. A possible juvenile specimen is represented by a left horn

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Plate 23 (Scale = 50 mm)

Parmularius angusticornis

Fig. 1 Anterior view of frontlet, HWK EE II 1972.172.

Fig. 2 Medial view of right horn core, HWK EE II 1972.2180.

core F.3003 found on the surface in 1941. We were unable to find the cranium with horn cores from BK II East mentioned by Leakey (1965 : 55) in either Nairobi or Dar es Salaam. We have seen three fine pieces found in 1972 at HWK EE in middle Bed II. 172 and 635 are frontlets with complete horn cores, and 2180 is a complete right horn core (Pl. 23). The horn cores are almost straight in side view but with a very slight forward curvature in their distal half and a tiny backward bend at their tip.

Four interesting specimens from BK II are a partial frontlet with complete right horn core 1963.2499 (Pl. 25, fig. 3), a frontlet with nearly complete horn cores 1963.3178 (Pl. 24), a left horn core 1963.067/1650 and a complete right horn core BK II East 1961.068/6660. The first three are very long and not large in relation to the underlying skull parts. The basal thickening is not pronounced and is no more developed than in *P. altidens*, although here the thickening is of

Plate 24 (Scale = 50 mm)

Parmularius angusticornis. Anterior view of frontlet, BK II 1963.3178.

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Plate 25 (Scale = 50 mm)

Fig. 1 ***Damaliscus agelaius.*** Lateral view of cranium S.38 from Bed II.

Fig. 2 ***Parmularius altidens/angusticornis.*** Lateral view of cranium, FLKN II 1960.067/4951.

Fig. 3 ***Parmularius angusticornis.*** Lateral view of right horn core, BK II 1963.2499.

the whole horn core base rather than on the medial side, and the outer surface is more flattened just above the base. In side view the back of the horn core bases project rather markedly beyond the pedicels, again unlike *P. altidens*. There are pronounced transverse ridges in two of them, as already mentioned. Both 1963.2499 and 1963.3178 show increasing divergence towards the tips like SHK II 1957.1284, and the tip of 1963.2499 has an abrupt backward and outward twist. The fourth horn core, 068/6660, is very similar but somewhat shorter. Probably all these horn cores are of females.

Further specimens in London are the right horn core bases M 14547 from Bed II in 1931 and M 14525 said to have come from Bed I in 1931, the distal part of a horn core M 14552 from the surface of Bed II in 1931, a right horn core base with part of the frontal M 21424 from the surface of SHK II in 1935, the basal part of a left horn core M 21426 from the surface of DC II in 1935, most of a left horn core M 21427 found in 1935, a right horn core base M 29416 from the surface of SC II in 1935 and a number of unregistered horn cores which were surface finds in 1935 (two left horn cores from SC II, a left base from DC II, a left horn core and part of a right from BK II, a left horn core from MRC II and an incomplete right horn core from GHTK II). The small basal diameters of M 29416 give it an appearance like *P. altidens*. Two other London horn cores can be tentatively identified as *Parmularius* sp.; these are a horn core tip M 14523 from Bed I in 1931 and the base of a right horn core M 14538 from Bed I (according to its label and the register) or Bed II (written on horn core) in 1932.

A left horn core F.3001 P.P.F.5 in Nairobi, marked 'Bed II *in situ*' and recorded as *Parmularius* sp. indet. by Leakey (1965 : 60; pl. 77), can perhaps be regarded as a male *P. angusticornis*. It has little basal swelling and is larger and less transversely compressed than BK II specimens, with slightly more curvature, but has the same amount of divergence. The orbital rim is preserved, the parietal is very short and there is a small parietal boss. The specimen is clearly not hippotragine by the angle of the braincase on the frontal, too little transverse compression and the outward divergence of the horn core.

We believe that *Parmularius angusticornis* could be the direct congeneric descendant of *Parmularius altidens*. It differs from *P. altidens* in having larger and straighter horn cores and a more extremely shortened braincase (Fig. 26), the latter brought about either by posterior movement

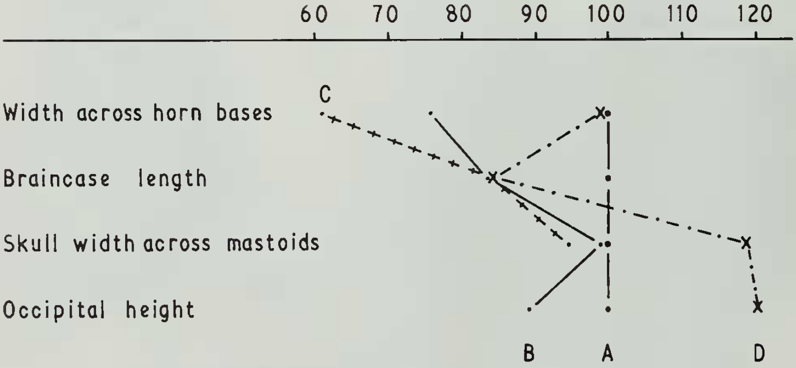

Fig. 26 Percentage diagram of skull measurements in some alcelaphines.

A = standard line at 100% for mean of 12 east African *Damaliscus lunatus*,
B = mean of 14 east African *Alcelaphus buselaphus cokei*,
C = *Parmularius altidens* holotype,
D = mean of 6 *P. angusticornis*: BK II 1955.P.P.T.1, 068/5854, F.3015, BM(NH) M 21428, M 21425, and Isimila cranium.

Braincase length is measured from the back of the frontals to the occipital top. *A. b. cokei* has closer horn core insertions, a shorter braincase and a lower occipital than *D. lunatus*. *P. altidens* has very close horn core insertions (connected with the small size of its horn cores) and a short braincase. *P. angusticornis* has a short braincase and a large occipital surface.

of the horn core insertions or by reorientation of the brain cavity internally. A possible intermediate stage is given by a cranium 1960.067/4951, with pieces of its horn cores 1960.067/4949, 067/4946 and 067/4948, from FLKN II 10 ft (3·05 m) above the base of Bed II (Pl. 25, fig. 2). It has the braincase top less shortened and less angled on the facial axis than in the SHK II and BK II *P. angusticornis*.

Leakey (1965 : 51), following Schwarz, placed *P. angusticornis* in *Damaliscus* but wrote 'there is no evidence to suggest that it is in any way ancestral to the living members of the genus. It has some characters that are nearer to *Alcelaphus* than to *Damaliscus*.' It is apparent that *Parmularius angusticornis* resembles *Alcelaphus* more than *Damaliscus* in the angle of nearly 90° between the planes of the frontals and the top of the braincase, the top of the braincase being set so steeply, and the extreme posterior position of the orbits; all these characters are linked with one another. Other resemblances to *Alcelaphus* are the horn core insertions being in the same plane as the face in side view, and the long distance of the horn core bases above the orbital rims. (In *A. buselaphus* the last character arises from the union of the horn core pedicels.) *Parmularius altidens* shows some of these resemblances: the obliquely inserted horn cores, long pedicels, horn cores parallel at least at their bases, and the characters connected with braincase shortening although at a less advanced stage. However, *Parmularius* is very unlikely to be ancestral to *Alcelaphus* because of its small preorbital fossae and extremely short premolar rows, and because of the existence of an alternative ancestor, *Rabaticeras* (p. 410), for *Alcelaphus*.

MEASUREMENTS. Measurements on the crania of *P. angusticornis* are:

	VEK II M.21428	SHK II M.21425	BK II 1955 P.P.T. 1	F.3015
Anteroposterior diameter of horn core at its base	62·0	61·4	58·1	–
Mediolateral diameter of horn core at its base	54·3	50·9	53·0	–
Minimum width across lateral surfaces of horn core pedicels	115·5	116·7	116·1	–
Width across lateral edges of supraorbital pits	64·6	–	66·6	–
Length from back of frontals to top of occiput	53·2	–	48·7	–
Maximum braincase width	100·5	–	103·0	101·0
Skull width at mastoids immediately behind external auditory meati	144·0	–	–	137·0
Occipital height from top of foramen magnum to top of occipital crest	–	59·6	58·4	60·9
Width of anterior tuberosities of basioccipital	29·1	–	–	32·9
Width of posterior tuberosities of basioccipital	46·9	–	–	40·7

Measurements on the two most complete frontlets of *P. angusticornis* are:

	HWK EE II 172	HWK EE II 635
Horn core length	280·0	305·0
Anteroposterior diameter at horn core base	68·2	66·1
Mediolateral diameter at horn core base	60·0	58·7
Minimum width across lateral surfaces of horn core pedicels	123·4	119·0
Width across lateral edges of supraorbital pits	73·4	–

Measurements on other frontlets of *P. angusticornis* are:

	VEK II M.21422	LONG K E II 068/6648	SHK II M.21423	BK II 1963.3178	068/5854
Anteroposterior diameter at horn core base	61·8	69·3	54·5	46·8	54·0
Mediolateral diameter at horn core base	55·1	57·4	43·8	38·4	45·6
Minimum width across lateral surfaces of horn core pedicels	127·4	126·4	113·6	90·5	116·1

Anteroposterior and mediolateral diameters at the base of other horn cores and one measurement of length on a horn core of *P. angusticornis* are:

HWK EE II 2180	63·0 × 59·1, length 340·0
SHK II 1952.598	52·7 × 41·5
SHK II 1957.945	57·6 × 48·7
SHK II 1957.1284	62·6 × 52·7
BK II 1963.2499	57·4 × 44·9
BK II 1963.2813	45·0 × 39·7
BK II 1963.067/1650	45·2 × 40·8
BK East II 1961.068/6660	46·0 × 40·8
Bed II F.3001 P.P.F.5	57·0 × 52·1
Bed II surface BM(NH) M 14553	58·0 × 49·5
BM(NH) M 21427	65·0 × 54·1

COMPARISONS. *Parmularius angusticornis* is represented at Peninj by the basal parts of left horn cores A67.254 (WN64.12.CFG III.MZ) and A67.253 (WN64.110.RDG.S), and a right horn core A67.243 (WN64.214.TMG(U) ?MZ), and possibly by other pieces. The anteroposterior and mediolateral diameters at the base of A67.243 are 60·5 × 55·0 mm.

Several pieces of *P. angusticornis* are known from Kanjera. BM(NH) M 15855 is the base of a horn core identified as *Alcelaphus kattwinkeli* by Hopwood (*in* Kent 1942 : 126), and there are also the distal ends of two more horn cores M 25626 and M 25722. The latter is preserved to the tip where it shows a sharp and localized backwards and inwards bend. M 25720 is a horn core base more doubtfully of *P. angusticornis*.

P. angusticornis is known from Isimila (Coryndon *et al.* 1972), a site in southern Tanzania equated with upper Bed IV of Olduvai by its Acheulian artefacts and perhaps about a quarter of a million years old (Howell & Clark 1963 : 482 and their references; Howell *et al.* 1972). This occurrence would therefore postdate its Olduvai record. The species is represented by a well-preserved cranium with both horn cores, at present in the Nairobi collections but eventually to be housed in Dar es Salaam.

Measurements on the Isimila cranium are:

Anteroposterior diameter of horn core at its base	59·7
Mediolateral diameter of horn core at its base	53·2
Minimum width across lateral surfaces of horn core pedicels	121·7
Length from back of frontals to top of occiput	56·3
Maximum braincase width	106·0
Skull width across mastoids immediately behind external auditory meati	130·0
Occipital height from top of foramen magnum to top of occipital crest	57·0
Width across posterior tuberosities of basioccipital	40·9

Langebaanweg horn cores previously recorded as *P. angusticornis* (Gentry *in* Hendey 1970a : 116) are now known to have been incorrectly identified. Subsequent finds show that not all horn cores have such clear basal swellings. Other characters are also unlike *P. angusticornis*: horn cores often curving more backwards, braincase roof less sharply angled, frontals lower between horn core bases and supraorbital pits closer together. In any case all the Langebaanweg alcelaphine teeth are less advanced than in Olduvai Bed II, and the fauna must be substantially earlier in age.

An incomplete cranium with both horn core bases, 1959.233 from Laetolil (Pl. 22, fig. 1) at present in Nairobi, has some resemblance to *P. angusticornis*. The horn cores arise close together beside the midfrontal suture and diverge at about 40°. The basioccipital, basisphenoid and a part of the occipital surface are present, but not the occipital condyles. It differs from *P. angusticornis* in the smaller size of its horn cores, their more upright insertions in side view, the insertions being less far above the level of the orbits or the supraorbital pits, the longer braincase roof less inclined downwards, there being no sign of a parietal boss, and in the narrower cranium. It could be related to the Langebaanweg species just mentioned, except that Laetolil alcelaphine teeth are more advanced than those at Langebaanweg. It is unlikely to be related to later *Parmularius* if the Laetolil skull 1959.277 (p. 382) is ancestral to *Parmularius*. 1959.233 differs from 1959.277 in its larger size, the slight forward bending indicated by the back of the right horn core, the absence of a parietal boss and the wider supraorbital pits.

Measurements on the Laetolil cranium 1959.233 are:

Anteroposterior diameter at base of horn core	47·6
Mediolateral diameter at base of horn core	42·7
Minimum width across lateral surfaces of horn core pedicels	110·1
Width across anterior tuberosities of basioccipital	25·2
Width across posterior tuberosities of basioccipital	33·8

Plate 26 (Scale = 50 mm)

Figs 1–2 ***Parmularius*** sp. Lateral and anterior views of cranium, 1965.068/5975 from Bed II.

Figs 3–4 ***Parmularius rugosus.*** Lateral and anterior views of right horn core, JK2 A.03 220 from Bed III.

Parmularius rugosus L. S. B. Leakey 1965

1965 *Parmularius rugosus* Leakey : 59; pls 75–76.

DIAGNOSIS. A species of *Parmularius* about the size of *P. altidens*, but horn cores diverging a short distance above the base and having a basal posterolateral swelling. Braincase roof about as short as in *P. altidens* but with only a small parietal boss; fairly small preorbital fossae; each side of the occipital facing partly laterally; small auditory bullae; basisphenoid bent upwards less strongly than in *P. angusticornis*.

HOLOTYPE. Skull with left and right P^4–M^3, BM(NH) M 21430, found in 1932.

HORIZON. The holotype came from the base of Bed IV at HWK Castle (M. D. Leakey 1971b : 287). Other specimens are from Bed III.

REMARKS. This species is less specialized morphologically and less common as a fossil than the larger *P. angusticornis* of Bed II. Unfortunately the holotype has retained only a part of its right horn core on which the posterolateral swelling is slightly indicated. It may have lacked at least the left P^2 in life, but this is not certain. It seems to have been correctly assigned generically, as indicated by its oblique horn core insertions situated close together, the posterolateral basal swelling of the horn core, short and strongly angled braincase, small parietal boss, not very widely spaced supraorbital pits, small preorbital fossae and short premolar row.

The lack of information about horn core morphology of the holotype makes it difficult to be certain about assigning other Olduvai specimens to this species. A cranium JK2 TT1, found in 1969 in Bed III, has retained both its horn cores, and the right one is almost complete. It is best identified as *Parmularius rugosus*. The horn cores are long, not mediolaterally compressed, with no flattened lateral surface or keels, transverse ridges are present distally and a slight posterolateral basal swelling is present. They are inserted far behind the orbits, inserted obliquely in side view and close together in front view, parallel at the base then acquiring an increased divergence which diminishes at the tip, and curving backwards only distally. The braincase is very short, much bent on the face axis and with some trace of a parietal boss, the supraorbital pits not visible, and the occipital faces partly laterally as well as backwards and shows a strong, median vertical ridge with flanking hollows. The auditory bullae are inflated and of small to moderate size.

A right horn core, JK2 A.03 220 from Bed III (Pl. 26, fig. 3) may also be taken as *P. rugosus*. It is small, apparently inserted well behind the orbits, with a pronounced posterolateral swelling, diverges quite strongly and then has an inwardly recurved tip. It has no mediolateral compression. There are transverse ridges distally and a normal alcelaphine long shallow postcornual groove. Its differences from the holotype are a fairly sharp diminution in thickness above the base, and a sharp backward curvature in side view.

A larger but otherwise similar basal part of a right horn core without a number was found at SHK II in 1952. It shows the posterolateral basal swelling, backward curvature, divergence and lack of mediolateral compression, but has transverse ridges from the base upwards. Its earlier level than the last specimen must make assignment to *P. rugosus* still more tentative, particularly as another species of the same genus, *P. angusticornis*, is well known from SHK II.

A partial cranium with horn cores, 068/5975 (Pl. 26, figs 1, 2) was found in 1965 at HWK EE in black sand about 3·7 m above the Sandy Conglomerate in middle Bed II. R. L. Hay confirmed (personal communication, March 1969) that the matrix was 'pyroxene-rich volcanic sandstone with a little quartz. Some of the pyroxene is euhedral. This is very probably from Bed II above the level of the Eolian Tuff (now Lemuta) Member.' The features which suggest that this specimen is a *Parmularius* are the short braincase top strongly angled on what would have been the line of the facial axis, a small parietal boss (about as strong as in *P. angusticornis*) and the very oblique horn core insertions on long pedicels. The horn cores diverge strongly outwards a short distance above their bases, but in side view they are in the same plane throughout their preserved length, bending neither backwards nor forwards. They have no mediolateral compression. There is no sign of any basal swelling on the horn cores, but there is a hint of a posteromedial keel at the edge of the somewhat flattened posterior surface. The occipital surface has a prominent median vertical ridge, and each half of the surface has quite a strong lateral-facing component. The basioccipital is typically alcelaphine with a central longitudinal groove and anterior tuberosities less wide than the posterior ones. It differs from the 1969 JK2 III TT 1 cranium in the posteromedial keel at the base of the horn core, the abrupt bend outwards of the horn cores close to their base, the narrower basioccipital, and probably in having less upright horn core insertions. The most that can be done with this specimen is to assign it to *Parmularius* sp.

Several horn cores from lower Bed II and the lower part of middle Bed II at Olduvai belong to a small-horned alcelaphine, seemingly related to *Parmularius rugosus*. A complete left horn core 58 (Pl. 32, fig. 3), complete right horn core 067/5523 and the distal half of a right horn core 54 all came from HWK lower Bed II in 1959–60. An immature frontlet with complete right horn core and basal half of the left 068/6649 (Pl. 32, fig. 2) was found in clay above the Sandy Conglomerate (and above level 5) at HWK East II in 1962. Two frontlets with complete horn cores, 2061 and 2181, and a right horn core 954 (probably a female) were from the Sandy Conglomerate at HWK EE II in 1972. In addition we have seen a cast, kindly supplied by Mrs Mary Leakey, of a complete right horn core with a small part of the cranial roof, HWK EE II 1972.285. Two left horn core bases are from Bed I; these are BM(NH) M 14516 found in 1931 and retaining a considerable part of the frontal, and the poorly-preserved M 29421 probably found in 1932.

The overall size of these horn cores might have been a little less than in *P. rugosus*. They are short and thick-set, without mediolateral compression or a flattened lateral surface, curving outwards immediately from the base, then bending backwards and upwards nearer the tips. They are set at a low angle in side view. They tend to have a diagonal-transverse ridge passing across the anteromedial part of the base, and in M 14516 the root of this ridge is so well marked as almost to become a keel recalling that of the cranium 068/5975. The posterior surface is flattened in HWK EE 954 and 2181 and in M 14516. There are also the normal transverse ridges in the middle of the horn cores. They are inserted far behind the orbits, and their pedicels and frontals show extensive sinuses. The dorsal parts of the orbital rims project strongly.

A horn core 1955 P.P.F.4 from the surface of FLK was figured by Leakey (1965: 65; pl. 88 which is a front view and not a side view as stated in the caption) and tentatively but mistakenly assigned to *Thaleroceros radiciformis*. The horn core is from the left side, and appears to have had a very low insertion angle. It is similar to the horn cores from the HWK sites, but lacks the diagonal-transverse ridge at its base. It remains unidentified.

The *Parmularius rugosus* of Beds III and IV could have descended from *P. angusticornis* by a slight diminution in size, the acquisition of greater outward bending of the horn cores, and a change in the position of the basal swelling of the horn cores. However, the Bed II fossils apparently of *P. rugosus* and the earlier fossils from the HWK area suggest that more probably the lineage was separate. Few changes would be needed to transform the HWK horn cores into *P. rugosus*, and they must represent either its direct ancestor or a racial variant of the lineage which chanced to be in the Olduvai region at that period.

MEASUREMENTS. Measurements on specimens of *P. rugosus* are:

	BM(NH) M 21430	JK2 III TT 1
Anteroposterior diameter at base of horn core	36·8	42·4
Mediolateral diameter at base of horn core	32·3	37·8
Minimum width across lateral surfaces of horn core pedicels	–	*c.* 93·1
Width across lateral edges of supraorbital pits	55·5	–
Length from back of frontals to top of occipital crest	–	*c.* 45·6
Length from back of frontals to back of occipital condyle	–	*c.* 93·0
Length from midfrontal suture at level of supraorbital pits to top of occipital crest	118·4	–
Skull width across mastoids immediately behind external auditory meati	116·3	116·0
Distance from rearmost point of occlusal surface of M^3 to back of occipital condyle	157·0	–
Occipital height from top of foramen magnum to top of occipital crest	39·7	43·9
Width across anterior tuberosities of basioccipital	26·5	32·7
Width across posterior tuberosities of basioccipital	33·5	33·8

Occlusal length M^1–M^3	61·6	–
Occlusal length M^2	22·7	–
Estimated occlusal length P^2–P^4	*c.* 23·2	–

The length of the horn core JK2 III A.03 220 is 228.0, and the basal anteroposterior and lateromedial diameters 47.7 × 36.9 mm.

Measurements on the cranium HWK EE 068/5975 are:

Anteroposterior diameter at base of horn core	39·9
Mediolateral diameter at base of horn core	39·7
Minimum width across lateral surfaces of horn core pedicels	92·4
Occipital height from top of foramen magnum to top of occipital crest	48·7
Width across anterior tuberosities of basioccipital	24·8
Width across posterior tuberosities of basioccipital	30·1

Measurements on the more complete horn cores from the HWK area are:

	HWK EE 2061	HWK EE 2181	HWK EE 954	HWK East 068/6649
Horn core length	215·0	180·0	180·0	–
Anteroposterior diameter at horn core base	50·2	37·6	24·3	30·3
Lateromedial diameter at horn core base	52·9	44·4	31·2	31·0
Minimum width across lateral surfaces of horn core pedicels	96·2	94·6	–	87·2

On HWK EE 2181 the width across the lateral edges of the supraorbital pits is 62·3, and the skull width across the posterior side of the orbits is *c.* 150 mm.

Anteroposterior and mediolateral diameters at the base of the other horn cores in this group are:

HWK II 58	42·7 × 45·0	FLK surface P.P.F.4	47·2 × 48·6
HWK EE II 285 (cast)	37·6 × 44·1	BM(NH) M 14516	40·0 × 49·2

COMPARISONS. Some Elandsfontein horn cores, including a pair SAM 20076, may be assignable to *Parmularius*. They are larger than *P. rugosus* with strong mediolateral compression, inserted uprightly above the orbits on high pedicels and close together, parallel at the base in anterior view, bent sharply backwards in the middle with a pronounced torsion which is clockwise on the right side, and with a swollen base of the medial side and a concavity on the lateral surface. This distinctive and puzzling set of characters leaves little alternative except a doubtful assignment to *Parmularius*.

Genus *DAMALISCUS* Sclater & Thomas 1894

TYPE SPECIES. *Damaliscus dorcas* (Pallas 1766).

GENERIC DIAGNOSIS. Medium-sized alcelaphines with high and narrow skulls; horn cores with fairly simple curvature, with transverse ridges, inserted over the back of the orbits, less far back on the skull and less obliquely set than in *Alcelaphus*. Torsion of the horn cores is only incipient and is anticlockwise on the right side. Braincase short but longer than in *Parmularius*; slight tendency to a parietal boss; supraorbital pits set widely apart; preorbital fossae fairly large and larger than in *Parmularius*; moderate to large-sized foramina ovalia; premolar rows fairly long in living species and P_2s often retained.

REMARKS. *Damaliscus* has fewer specialized characters than *Parmularius*. Its tendency to have a parietal boss opens the possibility of a common ancestry with *Parmularius*.

Damaliscus niro (Hopwood 1936)

1936 *Hippotragus niro* Hopwood : 640, no figure.

Plate 27 (Scale = 50 mm)

Damaliscus niro. Medial view of cast of left horn core and frontlet from Peninj, BM(NH) M 26546.

1937 *Hippotragus leucophaeus* subsp. Schwarz : 87; pl. 2, fig. 11.
1965 *Hippotragus niro* Leakey : 48; pls 54–55.
1965 *Hippotragus* cf. *niger* Leakey : 50.
1965 *Hippotragus* cf. *equinus* Leakey : 51 (in part).
1965 Other gazelles Leakey : 65(j) (except 473 from HWK II); pl. 86.
1965 Alcelaphini indet. Leakey : 66(e); pl. 92.
1965 *Damaliscus niro* Gentry : 335.

DIAGNOSIS. An alcelaphine about the size of *Damaliscus lunatus* or larger. Horn cores moderately long, strongly compressed mediolaterally especially distally (but less strongly compressed in some Olduvai specimens), frequently with flattened lateral and medial surfaces, the widest part of the cross-section situated anteriorly, inserted above the back of the orbits and obliquely in side view but more uprightly than in *D. lunatus*, divergent as much as in *D. lunatus korrigum* or more so, curved evenly backwards (or in some Olduvai specimens with a fairly abrupt change of course about half way along the horn core length), many examples with strong and widely spaced transverse ridges on the front surface. Horn core pedicels short compared with *Parmularius*; postcornual fossae shallow and rather long; braincase strongly angled on the facial axis; sometimes a slight indication of a parietal boss; orbital rims moderately projecting.

HOLOTYPE. Right horn core BM(NH) M 14561, found in 1931.

HORIZON. The holotype is from JK1 and 2, Bed III (M. D. Leakey 1971b : 283). Other specimens are common in middle Bed II to Bed IV at Olduvai. The species is known from Peninj, and from several sites in South Africa including Cornelia, Florisbad, probably Elandsfontein and possibly Mahemspan.

REMARKS. Specimens of *Damaliscus niro* in London are a left horn core BM(NH) M 29418 found on the surface at SHK II in 1935, left horn core M 21450 found on the surface of BK II in 1935, distal part of a horn core M 21453 which may belong to M 21450, two pieces of horn core M 14564 found in Bed IV in 1931, and part of a horn core M 14519 found in 1931 and said to be from DK I. Part of a horn core M 29417 from the surface of NGC in Bed IV may also be of *D. niro*. M 21450 and M 14564, with the Nairobi horn cores BK II 1953.067/5235 P.P.R.2 and F.971 from the surface of Bed IV in 1941, were recorded as *Hippotragus* cf. *niger* by Leakey (1965: 50). The piece of a horn core called *Hippotragus leucophaeus* subsp. by Schwarz (1937 : 87; pl. 2, fig. 11) was probably this species. It was lost in Munich during the Second World War, but Schwarz had noted that it was mediolaterally compressed above a thicker lower part.

D. niro was a common antelope in both east and southern Africa. The horn cores in London listed above, and in Nairobi the two horn cores known from SHK II, the right horn core BK II 1955.159, nearly all those in Beds III to IV, and the ones in South Africa all have very strong mediolateral compression and flattened medial and lateral surfaces. The widest part of the cross-section is situated anteriorly, they are curved evenly backwards, and have very marked and widely-spaced transverse ridges on the front surface. This is the morphological pattern found in the holotype. At the BK II site there occur two other horn core varieties which may doubtfully be included in *D. niro*. The first (type A) comprises left horn cores 1952.1495 and 067/5238 (Leakey 1965 : pl. 86, first and third from the left), right 1963.1774, base of right BK II Ext 140, left 1957.876 (Leakey 1965 : pl. 86, fourth from the left), distal end of left BK II Ext 1953.65, and parts of left 1952.254, 1957.49, 1963.067/1594 and BK II Ext 1953.64. A left horn core BK II 1953 (no number), a right tip BK II Ext 1953.139, and part of a right BM(NH) M 29420 of unknown site and horizon are also probably of type A. Type A horn cores have less strong mediolateral compression, flattening of the lateral surface alone, the widest part of the cross-section situated more posteriorly, a more marked change in backward curvature half way between base and tip, a tendency to upturned tips (as occurs in horn cores and especially the horn sheaths of living *D. dorcas* and *D. l. korrigum*), transverse ridges closer together, and a small posterolateral swelling at the base. 1952.1495 and BK II Ext 140 show that the horn core bases are too close to the orbits and the braincase roof is too little angled downwards for satisfactory assignment to *Parmularius*. Two of this sort of horn core also occur at JK2 III, a piece A.976 and part of a

Plate 28 (Scale marked in centimetres)

Fig. 1 ***Damaliscus niro*.** Lateral view of frontlet from Kranskraal near Mazelspoort, Bloemfontein, C.666.

Fig. 2 Anterior view of same.

right A.2348; the last one is more compressed than the Bed II examples. A horn core tip, HWK East II level 2 891, is also like type A but is a little less compressed; we have not assigned it to *D. niro*.

The second group at BK II (type B) comprises the right horn core 067/5237 (Leakey 1965: pl. 86, second from the left), left 1952.252, left 1952.253, left 1953.067/5236 P.P.F.3 (recorded as possibly alcelaphine by Leakey (1965: 66(e); pl. 92)), left BK II Ext 1953.66, left BK II Ext 1953.67, right 1957.365 (taken by Leakey (1965: 51) as *Hippotragus* cf. *equinus*), right 1957.877, left 1963.9, left 1963.408, most of a left 1963.2869 and the horn core base 1963.3043. These also show less mediolateral compression and the widest part of the cross-section situated more posteriorly. However, they have very little or no flattening of the lateral surface, the backward curvature is not so pronounced nor is there a sharp change in course half way along the length of the horn core, transverse ridges are less marked, and there is a swelling of the whole medial surface at the base rather as in *Parmularius angusticornis*.

It is difficult to know how to deal with these horn core varieties which can be assigned to no known alcelaphine other than *D. niro*. Type B could easily be regarded as *D. niro* females of middle Bed II times, and this would require only the reasonable supposition that the three SHK II horn cores are male. If type A horn cores were also females, one would need some additional theorizing. Could they be closer to an ancestral pattern formerly present in both sexes?

The horn cores of *D. niro* differ from those of *D. lunatus* and *D. dorcas* by their mediolateral compression, flattened medial surface, very strong and more widely spaced transverse ridges, smaller increase in divergence from the base upwards, more upright insertions with the appearance of being more directly over the orbits and closer to the supraorbital pits, shallower postcornual fossae, and hollowing of the frontals extending less high above the pedicel top. The lyration of *D. dorcas* horn cores is not found in *D. niro*, and even the greater mediolateral compression of the horn cores of west African populations of *D. lunatus* is exceeded in *D. niro*. Horn cores of the two living species tend to have flattened lateral surfaces (not in *D. l. lunatus*) and the widest transverse diameter lies anteriorly or centrally, so in these two characters they are like *D. niro*. They often have transverse ridges, and these may be more evident distally.

MEASUREMENTS. Anteroposterior and mediolateral basal diameters and lengths of horn cores of *D. niro* are:

SHK II 1953.282	58·8 × 49·4
SHK II surface BM(NH) M 29418	58·6 × 44.1
BK II 1955.159	67·1 × 51·6
BK II surface BM(NH) M 21450	56·9 × 43·3
Elephant K II surface 1963.068/5920	65·8 × 49·9
JK2 III A.1130	57·0 × 48·3
JK1 and 2 III BM(NH) M 14561	58·1 × 45·7
JK2 III 1963	55·9 × 42·5, length 460·0
JK2 GP8 III 674	65·7 × 47·8, length 455·0
JK2 GP8 III 1627a	61·0 × –, length 485·0

The width across the lateral edges of the supraorbital pits of JK2 GP8 III 674 is *c.* 61·2 mm.

Anteroposterior and mediolateral basal diameters and lengths of type A horn cores from BK II are:

067/5238	47·8 × 36·4, length 253·0
1952.1495	50·9 × 39·6, length 335·0
1957.876	46·0 × 37·2, length 253·0
1963.1774	43·5 × 33·8, length 230·0
BK II Ext 140	52·0 × 39·6

Anteroposterior and mediolateral diameters at the base and length of type B horn cores from BK II are:

067/5237	46·9 × 36·4
1952.252	49·7 × 39·4, length 335·0
1957.365	52·3 × 41·6
1957.877	length 345·0
1963.9	49·7 × 38·9, length 315·0.

COMPARISONS. *D. niro* occurs at Peninj, and it was on a very large left horn core with part of the cranium attached from that site, A67.229 (WN64.174.CFG III.MZ), that the generic identity was established (Gentry 1965 : 335). The Peninj specimen (Pl. 27) has less extreme flattening of the medial and lateral surfaces of the horn core than in the most 'advanced' ones at Olduvai. This helps to link these horn cores with type B horn cores at BK II. The parietal is sufficiently preserved to be fairly certain that there was no boss or tuberosity in its centre.

Measurements on this horn core are:

Anteroposterior diameter of horn core at its base	64·2
Mediolateral diameter of horn core at its base	50·9
Width across lateral edges of supraorbital pits	62·9

A cast of the Peninj specimen is in London, BM(NH) M 26546; the horn core tip is not present on the fossil but has been artificially restored on the cast. A right horn core base with the mid-frontal suture and part of the orbit, A67.236 (WN63.390), also represents *D. niro* at Peninj. Its anteroposterior and mediolateral diameters are 63.9 and 51.3 mm. A horn core base A67.231 (WN64.239.JHG ? ?USC) may be of this species.

There is good representation of *D. niro* in South Africa. The most complete specimen is a cranium with the left and part of the right horn core C.666 from the Modder River, Kranskraal 134, near Mazelspoort, Bloemfontein district, in the National Museum, Bloemfontein (Pl. 28). It shows the horn cores to be strongly compressed above the basal part, inserted above the orbits and with flattened medial and lateral surfaces, the braincase bent on the facial axis, a small forward indentation centrally in the parietofrontals suture, small supraorbital pits which are wide apart, frontals raised between the horn core bases, and a parietal boss developed about as much as in living *Damaliscus* and therefore a lot less than in *Parmularius altidens*.

Measurements on the Kranskraal cranium C.666 are:

Anteroposterior diameter of horn core at its base	47·5
Mediolateral diameter of horn core at its base	43·3
Minimum width across lateral surfaces of horn core pedicels	96·4
Width across lateral edges of supraorbital pits	56·0
Maximum braincase width	73·3

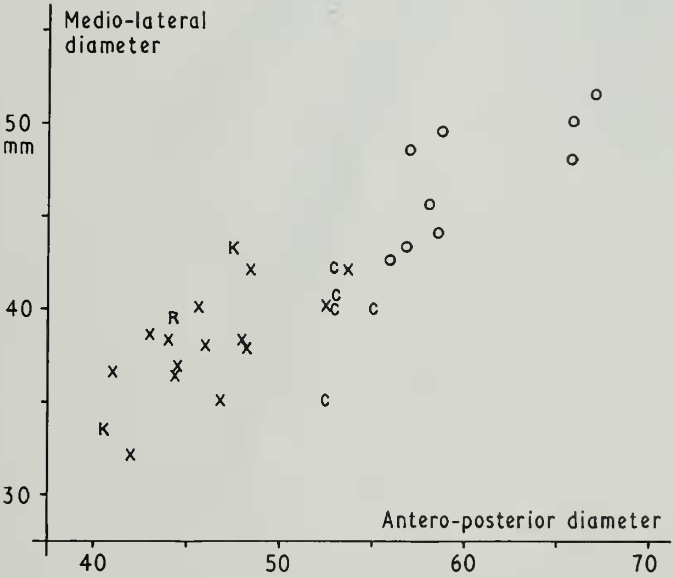

Fig. 27 Basal horn core dimensions of *Damaliscus niro*.
O = Olduvai Gorge, C = Cornelia, X = Florisbad, K = Kranskraal, R = Rustfontein.
There appears to be a size diminution in the later part of the species' temporal range.

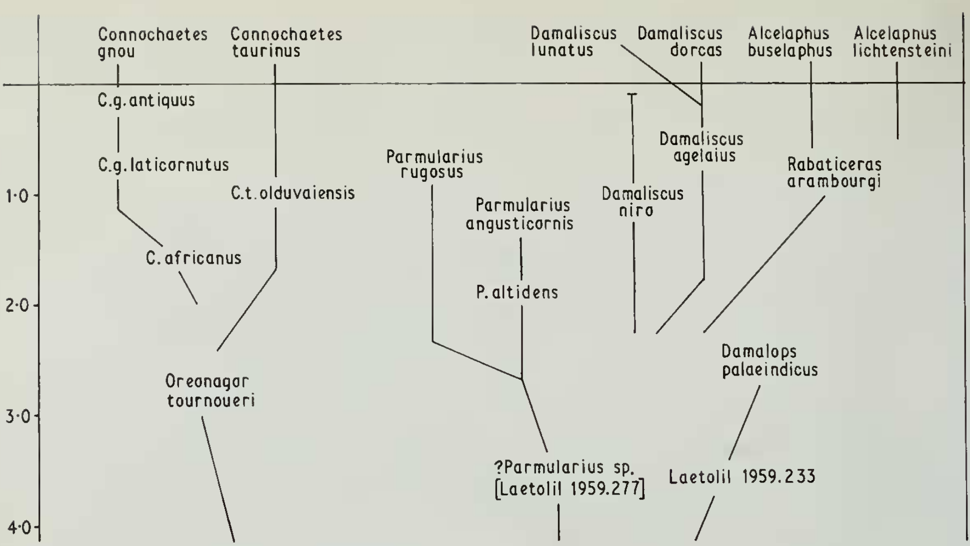

Fig. 28 Suggested phylogeny for alcelaphines of the *Connochaetes*, *Parmularius* and *Alcelaphus*/*Damaliscus* groups. Living species are shown above the horizontal line, and age is shown on the left in millions of years.

There is also a horn core C.643 from Kranskraal, 12 horn cores from Florisbad (all numbered C.1457), six from Cornelia (five numbered C.770 and one C.2864), three from Rustfontein (C.2756, C.2757 and C.2758), one from Vlakkraal (C.1542), some doubtful horn cores and small mandibles from Mahemspan, and possibly two horn cores from Elandsfontein (8560 and 20043). The horn from the Wonderwerk Cave described by Wells (1943 : 268) as cf. *Capra walie* belongs to *D. niro*. Wells (1970) also reports *D. niro* from Driefontein in the Cape Province. The Florisbad horn cores are smaller than those from Cornelia, and even the latter are smaller than the very large East African specimen from Peninj (Fig. 27). None show the abrupt bending back in mid course seen in many of the Olduvai Bed II horn cores assigned to *D. niro*. It is interesting that only two possible horn cores of this species are known from Elandsfontein.

Since the size diminishes in passing from Cornelia to Florisbad one wonders whether the species recently became extinct or whether it was transformed into *D. dorcas*. The former seems more likely on the present insubstantial evidence. A left horn core C.2930 from Florisbad has been noticed by Wells & Cooke (ms.) as possibly the blesbok, and we found two very similar horn cores in Cape Town, also from Florisbad, a right 3462 and a left 3464. Neither the inclination nor divergence of insertions can be assessed on these horn cores. They are larger than *D. niro* at the same site, the medial surface is more rounded and the whole horn core less compressed mediolaterally, the widest part of the transverse section is less anteriorly placed, and they have a slight alteration in course (lyration) seen in anterior view near the base. They differ from *D. dorcas* in their larger size, less mediolateral compression, and in the lyration lying nearer to the base, but are entirely suitable as ancestors. From Vlakkraal there are a left and two right horn cores (all numbered C.1540) of the Florisbad species like *D. dorcas* and a right horn core (C.1542) of *D. niro*. The three former are smaller than the Florisbad examples, and show more oblique insertions than *D. niro* and a high-extended hollowing in the pedicel. Horn cores of the living *D. lunatus lunatus* have little or no mediolateral compression and no flattening of the lateral surface. Perhaps they share with *D. dorcas* and the Florisbad horn cores C.2930, 3462 and 3464 a descent from *D. agelaius* (p. 402), and neither comes from the longer-separated lineage of *D. niro*. However, this is a tentative hypothesis and it is unfortunate that there is not a single complete tooth row known to be of *D. niro* from any African site.

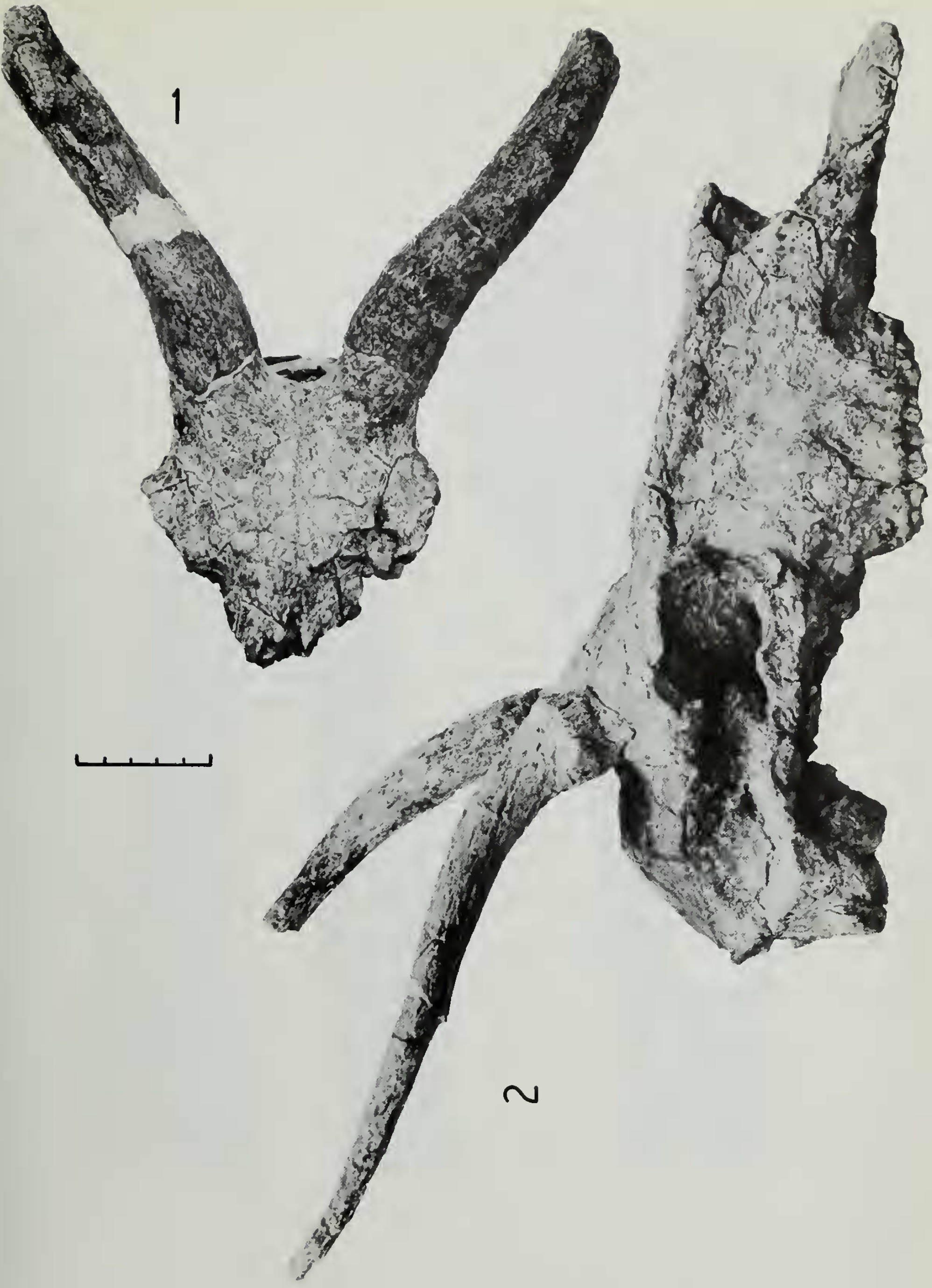

Plate 29 (Scale = 50 mm)

Damaliscus agelaius

Fig. 1 Anterior view of male cranium, VFK III–IV 214.

Fig. 2 Lateral view of holotype female skull, VFK III–IV 350.

The horn cores of the Laetolil cranium 1959.277, already mentioned in the account of *Parmularius altidens*, have some features in common with the type A horn cores of *Damaliscus niro* from BK II. They are a little compressed mediolaterally, the widest part of the cross-section is not situated anteriorly, there is a marked change in backward curvature just over half way between base and tip and a posterolateral swelling at the base. They differ in the absence of transverse ridges or clear flattening of the lateral surface, and more interestingly in the presence of a higher horn core pedicel. A horn core L.292-29 from member C of the Shungura Formation has some similar features to the Laetolil fossil and to *D. niro* type A horn cores. It is somewhat damaged at the base, but shows very slight mediolateral compression, the widest part of the transverse section not situated anteriorly, marked backward curvature near its middle, transverse ridges and an upturned tip. The lateral surface appears not to have been flattened. The parietal boss of the Laetolil cranium is also a resemblance to the *Damaliscus niro* partial cranium shown in Plate 28. There is little use in pursuing this discussion any further because of the uncertain identity of the BK II type A horn cores, and our ignorance of so much of the cranial morphology of *D. niro*. We can conclude only that 1959.277 points to the possibility of an immediate common ancestry for *Parmularius* and *Damaliscus niro* (but see also p. 412). A tentative phylogeny is shown in Fig. 28.

Damaliscus agelaius sp. nov.

Diagnosis. A species of *Damaliscus* smaller than *D. lunatus* and about the size of *D. dorcas*; horn cores smaller than in *D. dorcas*, moderately long and little compressed, inserted closer together and more uprightly than in living *Damaliscus*, in the males diverging to an extent intermediate between *D. lunatus lunatus* and *D. l. korrigum* and in the females less divergent, a few with transverse ridges but none with flattening of the medial or lateral surfaces. Frontals less convex in front of the horn core bases than in living *Damaliscus* and less uparched between the horn core bases than in *D. dorcas*; braincase longer than in living *Damaliscus*; no indication of a parietal boss; supraorbital pits as wide apart as in the living species; no ethmoidal fissures; deeper preorbital fossae than in *D. dorcas*; basioccipital rather short; auditory bullae more inflated than in *D. dorcas*; occlusal complexity of cheek teeth less than in living *Damaliscus*; premolar rows shorter than in living *Damaliscus*; P_2s absent.

Holotype. Female skull 350 with complete horn cores, maxillae and associated mandibles excavated from Fifth Fault Korongo (site VFK) in 1962 (Pl. 29, fig. 2). It is in the National Museum of Kenya, Nairobi.

Horizon. The holotype and other members of a fossilized herd of which it was a member came from Beds III–IV in an area of the Gorge where these Beds are not divisible (M. D. Leakey 1971b : 282). A few other specimens come from Beds II to III–IV.

Remarks. This species is noteworthy for possessing so few specialized characters. The specific name is taken from the Greek ἀγελαῖος (agelaios), with the meaning 'belonging to a herd'. The herd in question was found embedded in a clay matrix (Leakey 1965 : 107). Most of the skulls are complete but rather crushed, often in a transverse plane. There are about 16 skulls of which one, a cranium 214 (Pl. 29, fig. 1), is male. The horn cores have moderately long pedicels and are inserted fairly close together and above the back of the orbits. The suture of the parieto-frontals has no central anteriorly-directed indentation. Skull characters which are typically alcelaphine are the anterior thickening of the zygomatic arch, the position of the infraorbital foramen, shape of the mastoid exposure, the median indentation at the back of the palate passing to a level just anterior to the lateral ones, the long nasals, the premaxillae having an even width and contacting the nasals, the occipital surface in two planes with a median vertical ridge, and the basioccipital with a central longitudinal groove and no constriction across its centre.

A male cranium with incomplete horn cores, S.38, was found *in situ* at geologic locality 54 in 1968 (Pl. 25, fig. 1). That it is almost certainly from Bed II above the Lemuta Member is shown by the relatively high augite content and a small number of altered fragments of mafic volcanic glass in the matrix (R. L. Hay, personal communication, September 1973). It is not at all crushed and shows without doubt that this species had a longer braincase than living *Damaliscus*.

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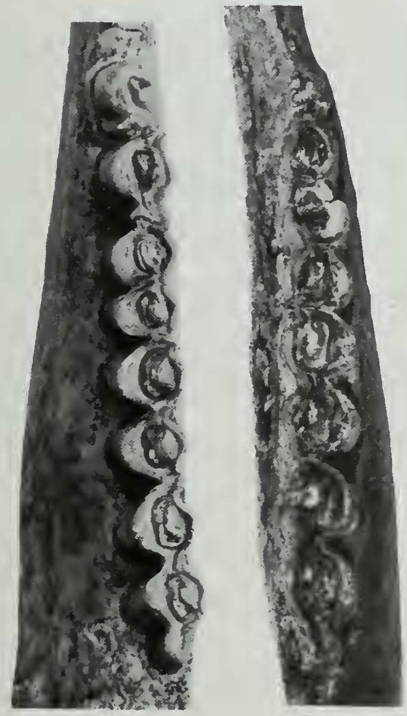

Plate 30 (Scale = 50 mm for skull and 25 mm for teeth)

Fig. 1 ***Damaliscus agelaius.*** Palatal view of skull, VFK III–IV 357.

Fig. 2 Lower left dentition of ***Damaliscus agelaius*** VFK III–IV 363 (left) compared with lower right dentition of ***Parmularius altidens*** FLKN I 1109 (right).

FLKW 1969.82a is an alcelaphine skeleton with the skull represented by a crushed cranium with horn cores. It was found above Tuff IF in greenish clays below the Sandy Conglomerate west of FLK. Some antilopine limb bones were found in association, for example a right metatarsal and a proximal right tibia. The skull is about the same size or even marginally larger than those of the VFK herd. It appears to be *D. agelaius* in its relatively small horn cores, their upright insertions above the backs of the orbits, the length and inclination of the braincase roof, and there being scarcely any sign of a parietal boss. The femur is rather short. The crushing forbids the assessment of further characters. This skull and skeleton is the earliest known representative of the species.

Other specimens are a left horn core A.1446 found in 1962, a partial horn core marked '1961 B.T.T.F. Floor', both female, and probably a distal half of a horn core A.345, all from JK2 III. In addition there is a right horn core with the frontal suture and orbital rim 068/6661 found on the surface at Hoopoe Gully in 1962 which has the robustness and divergence appropriate for a male of this species, and a male frontlet 068/5730 found in 1961 and labelled XDK. According to R. L. Hay (personal communication, September 1973) matrix from inside the horn core of 068/6661 was a light olive-grey claystone, locally sandy, and quartzose sand. Outside was a calcareous quartzose sandstone. The horn core is most likely to have originated from Beds III–IV (undivided), but Bed II cannot be excluded. The matrix of 068/5730 was a quartzose sandy limestone, and depending on provenance could be from Beds II, III, III–IV (undivided) or IV.

Damaliscus agelaius differs from its contemporary *Parmularius rugosus* in having horn cores inserted more uprightly in side view and less posteriorly on the skull, a longer braincase, less of a parietal boss, larger preorbital fossae, smaller teeth relative to the size of the skull, and less shortened premolar rows (Fig. 29). The species is smaller than *Damaliscus niro* and is without that

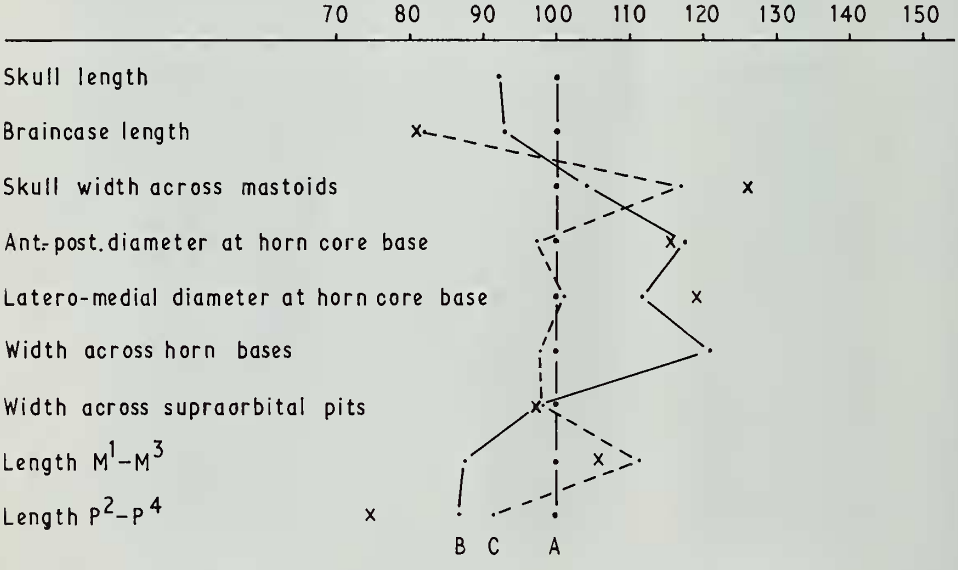

Fig. 29 Percentage diagram of some skull measurements in some alcelaphines.

A = standard line at 100% for mean of females in the Olduvai herd of *Damaliscus agelaius*.
B = mean for three female *D. dorcas dorcas* (except that the two horn core diameters are from a female *D. d. phillipsi*).
C = *Parmularius altidens* holotype.
Crosses = *P. rugosus* holotype.

Braincase length is measured from the back of the frontals to the occipital top. Compared with *D. agelaius*, *D. dorcas* has evolved a shorter braincase and larger, more compressed horn cores set wider apart. *Parmularius* species show a shorter braincase and a short premolar row.

species' distinctive characters of mediolaterally compressed horn cores with flattened medial and lateral surfaces and strong and widely spaced transverse ridges. On the whole the dentitions of *D. agelaius* are smaller than those presumed to belong to *D. niro*, although the ranges of the two species overlap. *D. agelaius* is a more likely ancestor for *D. lunatus* than is *D. niro*, and may be ancestral to *D. dorcas* as well. However, all the mandibles of *D. agelaius* lack an alveolus in the jaw for a P_2 and this may preclude it from ancestry to living *Damaliscus*. P_2 is still customarily present in *D. lunatus*, while in a sample of *D. dorcas* 18 individuals have P_2 and 11 do not. R. G. Klein, who supplied information on *D. dorcas* from the collections of the South African Museum, believes that P_2s tend to be lost with increasing ontogenetic age.

Measurements. Measurements on the more complete skulls of the VFK III–IV herd and the cranium S.38 from geologic locality 54, Bed II, of *D. agelaius* are:

	350	150	235	363	214	S.38
	♀	♀	♀	♀	♂	♂
Skull length from front of the premaxillae to back of the occipital condyles . . .	347·0	–	–	319·0	–	–
Skull width across posterior side of orbits .	–	126·5	–	–	–	119·0
Length of horn core along its front edge .	247·0	–	235·0	–	–	–
Anteroposterior diameter of horn core at its base	30·2	–	29·2	31·4	39·2	–
Mediolateral diameter of horn core at its base	24·4	–	24·4	–	36·9	36·9
Minimum width across lateral surfaces of horn core pedicels	68·3	–	75·3	–	93·2	86·1
Width across lateral edges of supraorbital pits.	–	–	60·0	–	67·0	68·8
Length from back of frontals to top of occiput.	–	64·5	–	–	–	–
Maximum braincase width	–	72·8	–	–	75·0	75·3
Skull width at mastoids immediately behind external auditory meati	91·6	98·3	–	90·5	–	94·0
Occipital height from top of foramen magnum to top of occipital crest	–	34·3	–	34·3	–	–
Width of anterior tuberosities of basioccipital.	–	25·7	23·5	–	–	–
Width of posterior tuberosities of basioccipital	–	–	35·5	–	–	–
Occlusal length M^1–M^3	56·8	58·1	57·1	55·9	–	–
Occlusal length M^2	18·9	22·1	21·8	20·2	–	–
Occlusal length P^2–P^4	28·9	35·5	31·6	30·5	–	–
Occlusal length M_1–M_3	58·1	–	–	59·7	–	–
Occlusal length M_2	19·2	–	–	19·4	–	–
Occlusal length P_3–P_4	21·5	–	–	23·1	–	–

Measurements on 16 female horn cores of *D. agelaius*, including four from the skulls whose measurements are listed above, are:

	Number measured	Mean	Range	Standard deviation	Standard error
Length of horn core along its front edge.	6	236·0	220·0–266·0	22·0	9·10
Anteroposterior diameter of horn core at its base	15	31·8	29·2– 39·2	1·8	0·49
Mediolateral diameter of horn core at its base	15	27·1	23·6– 36·9	2·6	0·76
Minimum width across lateral surfaces of horn core pedicels	7	73·9	68·3– 93·2	4·4	1·97

The JK2 III–IV horn cores are not measurable. The anteroposterior and mediolateral basal diameters of 1962.068/6661 from Hoopoe Gully are 35·7 × 29·9 mm.

Measurements on 15 maxillae of *D. agelaius*, including four from the skulls whose measurements are listed above, are:

	Number measured	Mean	Range	Standard deviation	Standard error
Occlusal length M^1–M^3	14	58·2	55·0–62·3	2·1	0·57
Occlusal length M^2	14	20·8	18·9–22·5	1·1	0·29
Occlusal length P^2–P^4	10	31·0	29·2–35·3	1·9	0·61

Measurements on six mandibles of *D. agelaius*, including two from the skulls whose measurements are listed above, are:

	Number measured	Mean	Range	Standard deviation	Standard error
Occlusal length M_1–M_3	5	61·8	58·1–65·1	3·0	1·35
Occlusal length M_2	6	20·0	19·2–21·4	0·8	0·32
Occlusal length P_3–P_4	5	22·4	21·5–23·4	0·8	0·36

Measurements on the skull of FLKW 1969.82a are:

Anteroposterior diameter of horn core at its base	*c*. 35·0
Length from back of frontals to top of occiput	*c*. 80.0
Width of anterior tuberosities of basioccipital	24·5
Width of posterior tuberosities of basioccipital	*c*. 34·0
Occlusal length M_1–M_3	*c*. 62·0
Occlusal length M_2	19·3
Occlusal length M_3	26·0
Occlusal length P_3–P_4	*c*. 25·2
Occlusal length P_4	14·4

It is not clear whether or not P_2 was present in life.

Lengths and least thicknesses of the associated limb bones are:

Left femur	95	242 × 23·2	Left metatarsal	96	246 × 17·9
Left tibia	94	306 × 24·7	Left metacarpal	100	234 × 19·9

Comparisons. An alcelaphine about the size of *Damaliscus dorcas* or a little larger, from the Pinjor Formation of the Siwalik Hills, was referred by Pilgrim (1939 : 67) to *Damalops palaeindicus* (Falconer). The Pinjor Formation may be between two and three million years old by faunal correlation (Maglio 1973 : 70–71). Specimens in London are a damaged adult skull BM(NH) 39594, an immature skull 39598 figured by Lydekker (1886 : pl. 4, figs 3, 3a), an isolated right horn core thought to be from the same block of matrix as 39594, and a palate and paired mandibles 39571. In this species the slender horn cores are inserted fairly uprightly, they curve slightly backwards and have increasing divergence towards the tips, the cross-sectional long axis of the horn cores is set at an angle rather than nearly parallel to the long axis of the skull, the preorbital fossae are large and deep, the braincase is moderately angled on the facial axis, the premolar row is fairly long (a little less so than in living *Alcelaphus* and *Damaliscus*), P_2 is present, and P_4 has a fused paraconid and metaconid. The immature skull 39598 and Lydekker's illustration (1886 : pl. 4, fig. 5) of the holotype skull in Calcutta show that there is no parietal boss in this species. With the course of its horn cores, large preorbital fossae and the presence of P_2, *Damalops palaeindicus* may be related to the *Damaliscus–Alcelaphus* group. *Damaliscus agelaius* differs from it in its more upright horn core insertions, the longitudinal cross-section of the horn cores being more nearly parallel to the longitudinal axis of the skull, a less sloping dorsal part of the orbital rim, the braincase roof being perhaps less slanted, and a shorter premolar row arising mostly from the absence of P_2. It also existed in a later time span than *Damalops palaeindicus.*

Genus *RABATICERAS* Ennouchi 1953

1953 *Rabaticeras* Ennouchi : 126.

Type species. *Rabaticeras arambourgi* Ennouchi.

Generic diagnosis. As for the single species.

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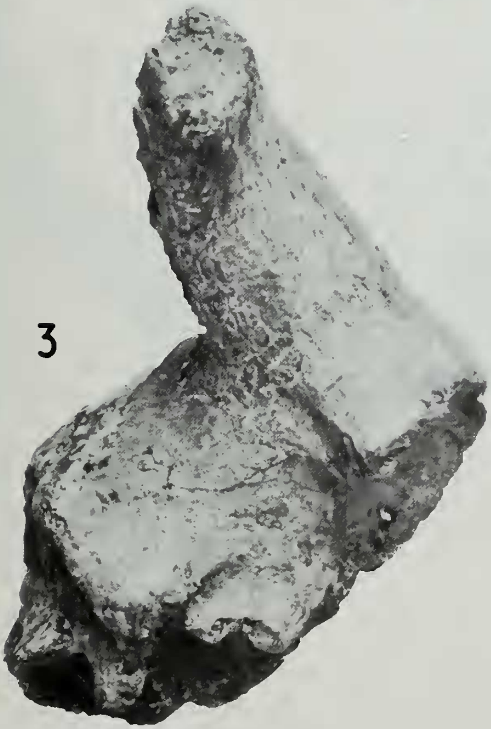

Plate 31 (Scale = 50 mm)

Fig. 1 ***Rabaticeras arambourgi.*** Anterior view of frontlet, JK2 III A.1129.

Fig. 2 ***Rabaticeras arambourgi.*** Lateral view of left horn core, JK2 III B.E/S K7-1.

Fig. 3 **Alcelaphini** sp. 2. Lateral view of cranium S.208 from Lemuta Tuff Member, lower Bed II.

Rabaticeras arambourgi Ennouchi 1953

1953 *Rabaticeras arambourgi* Ennouchi : 126, figs 1–2.

DIAGNOSIS. An alcelaphine with skull proportions nearer to high and narrow than to low and wide; horn cores moderately long, mediolaterally compressed, sometimes with a flattened lateral surface at least near the base and an approach to a posterolateral keel, inserted close together and above the back of the orbits, little divergent at the base but increasingly so in the middle part and then reapproaching at the tips, twisted in a clockwise direction in the right horn core[4], inserted quite uprightly in side view and curving forwards towards the tips; braincase strongly angled on the facial axis and with parallel sides. Frontals between the horn core bases at a higher level than the dorsal parts of the orbital rims; no parietal boss; moderately projecting orbital rims; occipital surface almost in one backward-facing plane with a slight vertical ridge and no hollows on either side; foramina ovalia small to moderate-sized.

HOLOTYPE. A frontlet with the basal halves of both horn cores, collected in 1951, number 29 in Rabat.

HORIZON. The holotype came from a sandstone in Quarry 8 on the coastal road from Rabat to Témara, Morocco, and further conspecific pieces from overlying red clays at Bou Knadel, 20 km north of Quarry 8. These occurrences might range as late as Soltanian in age, so that Middle–Upper Pleistocene is a possible age for *R. arambourgi* in Morocco. Details of Moroccan geological and climatic successions are given in Biberson (1967 : 361; 1971) but the level of *R. arambourgi* has not been established. The main difficulty arises from the frequent use of the expression 'the Rabat sandstone' in the literature, since there are a number of sandstones at Rabat ranging from lower to terminal Pleistocene (Biberson, personal communication).

Remains inseparable from the holotype come from Bed III and probably Bed IV at Olduvai and it is common at Elandsfontein. A similar animal comes from Bed II at Olduvai (see p. 417), and a further one from Swartkrans.

REMARKS. The best two Olduvai specimens of this species are from JK2 in Bed III. These are a frontlet A.1129 with both orbital rims and the proximal half of the right horn core, and an almost complete left horn core B.E/S K7-1 with the frontal, parietal, complete orbital rim and supraorbital pit (Pl. 31, figs 1, 2). The mid-frontal and parietofrontal sutures are not very complicated, and there is no indentation in the middle of the parietofrontal suture. A fragmentary left horn core A.346 may be the same species. It is also probable that a left horn core with part of the frontal PDK IV 1970.1498 belongs to *R. arambourgi.* The Olduvai material cannot be distinguished from the Moroccan species. A specimen from Morocco was given to the Institut de Paléontologie in Paris by M. Ennouchi and a cast of this fossil was kindly sent to us by Mlle Signeux and is now in the British Museum (Natural History), M 31901. It is a frontlet with complete left horn core, frontals with supraorbital pits and a small part of the braincase roof, and seems to be smaller than the holotype. It is about the size of a hartebeest and the horn core is moderately long and mediolaterally compressed with a flattened lateral surface and approach to a posterolateral keel, twisted in an anticlockwise direction, inserted rather uprightly, close to the midline and above the back of the orbits, little divergent at the base but increasing in the middle part and then reapproaching at the tip. The braincase is strongly angled on the facial axis and the frontals between the horn core bases are higher than the top of the orbital rims. Since the horn cores of *Rabaticeras* are inserted more anteriorly than in *Parmularius*, there can be no doubt that the steep angle of the braincase roof in profile must be linked with reorientation of the brain cavity internally.

Ennouchi thought that his new frontlet was a caprine. However, both the Olduvai frontlet and Elandsfontein specimens show that the horn cores are not hollowed, there are no caprine teeth at either Olduvai or Elandsfontein, and the basioccipital on an Elandsfontein cranium is typically

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[4] Following the observations of Vrba (1971 : 62), we would like to extend the list of Gentry (1970a : 274) of bovids in which torsion of the horn cores is clockwise on the right side to comprise *Menelikia*, *Megalotragus*, *Connochaetes*, *Oreonagor*, *Alcelaphus*, *Rabaticeras*, *Antidorcas*, *Sinotragus*, *Ovibos*, *Parurmiatherium*, *Bootherium*, *Euceratherium*, *Benicerus*, *Oioceros*, *Sivacapra*, most *Ovis* and some Bovini.

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Plate 32 (Scale = 50 mm)

Fig. 1 **Alcelaphini** sp. 2. Anterior view of cranium S.208 from Lemuta Tuff Member, lower Bed II.

Fig. 2 ***Parmularius*** aff. ***rugosus***. Anterior view of immature frontlet, HWK East 1962.068/6649 from middle Bed II.

Fig. 3 ***Parmularius*** aff. ***rugosus***. Anterior view of left horn core, HWK 1960.58 from lower Bed II.

alcelaphine and unlike caprines in its central longitudinal groove and anterior tuberosities about as wide instead of wider than the posterior ones. The tendency to a posterolateral keel can be matched among caprines only in *Capra falconeri*, the horn cores of which do not otherwise resemble *R. arambourgi*.

R. arambourgi is a good candidate for the ancestry of the living hartebeest *Alcelaphus buselaphus*. The fossil horn cores differ from the South African *A. buselaphus caama* only in their more upright insertions, less divergence, less abrupt alterations in course (in particular the lack of a sharp backward bend at the tips) and the absence of the long united pedicel. Also the braincase has parallel sides instead of widening posteriorly. The evolution of the united pedicel and the sharper curvature of the horn cores of *A. buselaphus* must have taken place very rapidly since Olduvai Bed III and Elandsfontein times. Similarly fast evolution has already been postulated for *Connochaetes gnou* (p. 365). It is interesting that the three localities for *Rabaticeras* are within the wide geographical range of living or recently exterminated *A. buselaphus* populations. It is apparent from the dating of the Olduvai beds that if *Rabaticeras* is ancestral to *Alcelaphus*, then this lineage is unlikely to have split from *Damaliscus* less than one million years ago. This is interesting in relation to the recorded hybridization between living species of *Damaliscus* and *Alcelaphus*. If further finds substantiate the connection between *Rabaticeras* and *Alcelaphus*, it would become appropriate to abandon *Rabaticeras* as a separate genus.

MEASUREMENTS. Measurements on the two Bed III specimens of *R. arambourgi* and the frontlet in Paris are:

	JK2 A.1129	JK2 B.E/S K7–1	Paris
Skull width across posterior side of orbits	152·0	–	–
Anteroposterior diameter at horn core base	47·5	47·0	*c.* 42·0
Lateromedial diameter at horn core base	41·4	39·5	*c.* 32·0
Minimum width across lateral surfaces of horn core pedicels .	99·4	–	84·0
Width across lateral edges of supraorbital pits	70·8	–	58·3

The horn core PDK IV 1498 has anteroposterior and lateromedial basal diameters of 37·1 and *c.* 34 mm.

COMPARISONS. *Rabaticeras arambourgi* is a very common antelope at Elandsfontein. Its remains include a cranium with the bases of both horn cores 9470, a complete right horn core with the frontal 4498, a number of frontlets and many horn cores. The cranium has a narrow and strongly angled braincase with an alcelaphine-like basioccipital. The Elandsfontein material appears to be from a slightly smaller animal than at Olduvai, and the measurements of the Moroccan specimen fall within the Elandsfontein range.

Vrba (1971) has described from Swartkrans, South Africa, an antelope frontlet like *R. arambourgi* but larger and with proportionally smaller horn cores. She believed it to be a new species and thought at that time that it could best be referred to *Damaliscus*. Accordingly she proposed the name *Damaliscus porrocornutus* for the Swartkrans species. We may expect the future discovery of a greater range of infraspecific and supraspecific regional variation in *Rabaticeras*.

Alcelaphus buselaphus is known from late north-west African sites. Arambourg (1938 : 37) considered that Pomel's names *Boselaphus probubalis*, *B. saldensis* and *B. ambiguus* were all referable to this species. The shape of the horn cores on a frontlet of *B. probubalis* from Aboukir, Algeria (Pomel 1894 : pl. 4, figs 14–15), suggest in their anterior aspect that they could be from an ancestor of the extinct north African race, *A. buselaphus buselaphus*. However, in side view the horn cores have more forward curvature proximally and less backward curvature distally than living hartebeests, and *probubalis* might as easily be a subspecies of *Rabaticeras arambourgi* as of *Alcelaphus buselaphus*. Further examination of the fossils in question is desirable. Aboukir is thought to be of Amirian (= Middle Pleistocene) age. References to *Alcelaphus* at earlier sites, for example Arambourg's (1962 : 106) report for Ternifine, are probably based only on teeth and may be discounted. An alcelaphine, which was most probably *Alcelaphus buselaphus*, occurred in the recent past in Palestine, Jordan and more doubtfully Lebanon (Garrod & Bate 1937 : 215, fig. 7g and h; Ducos 1968 : 49, pl. 10; Clutton-Brock 1970 : 26; Hooijer 1961 : 45, pl. 2, fig. 2).

Alcelaphus lichtensteini or an immediately ancestral species is represented at Broken Hill,

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Plate 33 (Scale = 50 mm)

Fig. 1 ***Beatragus antiquus*** holotype. Anterior view of right horn core from Bed I, BM(NH) M 21445.

Fig. 2 Medial view of same.

Zambia, among material previously assigned to *Connochaetes* (Leakey *in* Clark 1959 : 230). There is a base of a left and most of a right horn core BM(NH) M 12144, a left horn core M 12910 and two tips M 29486 and M 29487. The middle part of the right horn core curves sharply upwards, increases its thickness as it rises and shows transverse ridges towards the back of the dorsal side. Compared with *A. lichtensteini* it is very large and the top of the middle part is less twisted backwards towards the tip. This last character takes it closer to the supposed *Rabaticeras* ancestor, but one should not place too much weight on so slight a character.

The Pinjor Formation alcelaphine *Damalops palaeindicus* has already been compared with *Damaliscus agelaius* and was held to be related to the *Alcelaphus–Damaliscus* group. It differs from *Rabaticeras arambourgi* by the backward curvature of its horn cores in side view, the greater slope of the dorsal parts of the orbital rim, and probably by its less strongly sloping braincase roof. The horn core insertions also appear to lie further behind the orbits, which is probably linked with their being less upright. The absence of a parietal boss could imply that it is closer to *Rabaticeras* and *Alcelaphus* than to *Damaliscus*, and in this case the *Alcelaphus* lineage would become the only alcelaphine stock known to have existed outside Africa. For the moment this conclusion would be premature.

It is interesting that *Damalops palaeindicus* appears to have a close resemblance to the Laetolil partial cranium 1959.233, mentioned earlier on p. 390. The details are not relevant to the present paper, but the resemblance leads to the problem that if *Damalops* is related to the *Alcelaphus–Damaliscus* stock, how can it be that *Damaliscus niro* has more resemblance to the Laetolil cranium 1959.277 than to 1959.233? Interbreeding is possible between species of *Damaliscus* and *Alcelaphus* today, and one would not welcome their ancestry having been separate as long ago as in the Laetolil fauna. Alternative solutions are possible of course, but they need not be discussed until more fossils become available. Meanwhile a tentative phylogeny is shown in Fig. 28 (p. 400).

Genus ***BEATRAGUS*** Heller 1912

Type species. *Beatragus hunteri* (P. L. Sclater 1889).

Generic diagnosis. Medium-sized alcelaphines with horn cores inserted fairly uprightly over the back of the orbits, diverging strongly near the base but with long straight distal parts which are nearly parallel to one another, and with their long axis of cross-section set at a wide angle to the midline of the skull and not almost parallel to it as in most antelopes; strong transverse ridges. Where torsion is detectable in the horn cores it is anticlockwise on the right side. Supraorbital pits wide apart; preorbital fossae smaller than in *Alcelaphus* or *Damaliscus* but in the living species not as small as in *Parmularius*; P_2 usually absent.

Beatragus antiquus L. S. B. Leakey 1965

1937 *Beatragus hunteri* Schwarz : 55; pl. 2, fig. 9.
1965 *Beatragus antiquus* Leakey : 61; pl. 80.

Diagnosis. A species of *Beatragus* differing from living *B. hunteri* in its larger size; horn cores with more upright insertions in side view, diverging from the very base, sometimes less mediolaterally compressed in their lower parts, and with a less abrupt alteration in their course above the initial outward divergence; frontals wider and more convex in front of the horn core bases and less uparched between them.

Holotype. The lower part of a right horn core with much of the frontal anterior to the base, BM(NH) M 21445 found in 1935 (Pl. 33).

Horizon. The holotype is from Bed I, Olduvai Gorge. A few other specimens are known from Beds I and II. The species is also known from high in member G in the Shungura Formation, Omo.

Remarks. The paratype is an almost complete left horn core M 21446 found in Bed I in 1935 (Leakey 1965 : 61; pl. 80), and is probably from the same individual as the holotype. Other specimens in London are an incomplete right horn core M 21454 found in HEK II in 1935 and identified by Professor Wells in 1963, and parts of left horn cores M 14526 found in 1931 in Bed I, M 14539 found in 1932 in Bed I and M 29422 found in 1931 possibly in Bed I. The lower part of a right horn core M 26927 with part of the frontal and orbital rim from the surface of Bed I in 1931 is also probably of this species, perhaps a female. Specimens in Nairobi are a complete left horn core FLKN I 5123; the proximal half of a right horn core FLKN I 7132; part of a right horn core from MJTK I found in 1963; the proximal half of a left horn core 1962.067/4998 from FLKN II (base of Bed II); the lower half of a right horn core HWK East II 131 from level 1 which may be another female (Pl. 12, fig. 1); a frontlet S.217 with a nearly complete left horn core and most of the right found in 1971 at HWK East II in the rootlet clay of level 2 (Pl. 34); and a complete right horn core 1962.068/6654 from Kit K, a site at the first fault in upper Bed II.

The horn cores are less mediolaterally compressed than in *B. hunteri*, and both the holotype and paratype differ from the living species in having a larger posterior swelling at the very base of the horn core. The holotype horn core is inserted more uprightly in side view than in *B. hunteri*, diverges more from its base instead of curving gradually outwards, has localized up-arching of the frontals between the horn core bases and probably has a wider skull. All these features are also visible on the frontlet S.217. The horn core FLKN I 5123 is larger and thicker than in *B. hunteri*; it is less mediolaterally compressed, more divergent from its base in anterior view, and bent less backwards near the base and less upwards near the tip in side view. The horn core Kit K II 068/6654 is larger and longer than *B. hunteri* horn cores, and is still thicker than 5123. It is more mediolaterally compressed than 5123, perhaps as much as *B. hunteri*, but like 5123 the base passes directly outwards and in side view the bending is less pronounced than in *B. hunteri*. Its distal part passes inwards in anterior view more than in *B. hunteri* or other fossils. The more complete preservation than in 5123 shows that the insertion is probably more upright than in *B. hunteri* and that, as in *B. hunteri*, there is a shallow postcornual groove.

The partial right horn core from Olduvai which Schwarz (1937 : 55; pl. 2, fig. 9) identified as *B. hunteri* was almost certainly this species. The specimen was in Munich and was destroyed in the Second World War.

Beatragus is a long-lasting lineage. It differs from *Alcelaphus* in the more upright horn core insertions and their less posterior position on the skull, and from *A. buselaphus* in the lack of a united horn core pedicel. The abrupt alterations in horn core course and the coat colour of the living species are unlike *Damaliscus*, and the loss of P_2 distinguishes it from both *Alcelaphus* and *Damaliscus*. However, the small preorbital fossae and reduced premolar rows are approaches to *Parmularius*. In all the fossil *Beatragus* the long axis of the cross-section of the horn core bases is set at a wide angle to the midline of the skull. The same character can be seen in males of the living species, and we have taken it as another character whereby *Beatragus* can be distinguished from other genera.

MEASUREMENTS. Anteroposterior and mediolateral diameters at the base of horn cores of *B. antiquus* are:

Bed I BM(NH) M 21445	64·5 × 64·2	HWK East II 131	43·6 × 44·3
Bed I surface BM(NH) M 26927	50·9 × 41·5	Kit K II 068/6654	65·8 × 67·2

The lengths of FLKN I 5123 and Kit K II 068/6654 are 530·0 and 505·0 mm.

Measurements on the frontlet S.217 from HWK East II are:

Anteroposterior diameter of horn core at its base	52·3
Mediolateral diameter of horn core at its base	61·5
Minimum width across lateral surfaces of horn core pedicels	132·6
Width across lateral edges of supraorbital pits	73·5

COMPARISONS. A well-preserved and probably sub-adult cranium, FG 27-1, with most of the right and base of the left horn core was found just below Tuff H of the Shungura Formation, Omo, in 1967. It is the most complete specimen of *B. antiquus* so far discovered, and shows that the extinct species was larger than the living, and had relatively wider frontals and more of a parietal boss.

Like the living species it had a suite of generalized alcelaphine characters: a short braincase with quite a steeply inclined roof, a suture of the parietofrontals which is not very indented centrally, a median vertical ridge with flanking hollows on the occipital, an occipital surface facing mainly backwards, a basioccipital with moderate development of anterior tuberosities and longitudinal ridges, rather large foramina ovalia and the basisphenoid not strongly angled on the basioccipital.

A Kaiso horn core with the inscription 'KAISO C.94' is accompanied by a label reading *Beatragus* cf. *antiquus*. It is probably the horn core referred to as BM(NH) M 26623 by Cooke & Coryndon (1970 : 213). It is not impossible that it is alcelaphine, but having strong transverse ridges and no sinuses visible in the preserved part of the pedicel, it may be reduncine. We would not feel sure of an attribution to *Beatragus*.

The only South African fossils which seem to be *Beatragus* are a frontlet 16561 and other horn cores from Elandsfontein. The frontlet is from an antelope about the size of a wildebeest and has horn cores with slight mediolateral compression, some flattening of the lateral surface, a trace of a

Plate 34 (Scale marked in centimetres)

***Beatragus antiquus*.** Anterior view of frontlet S.217 from HWK East II.

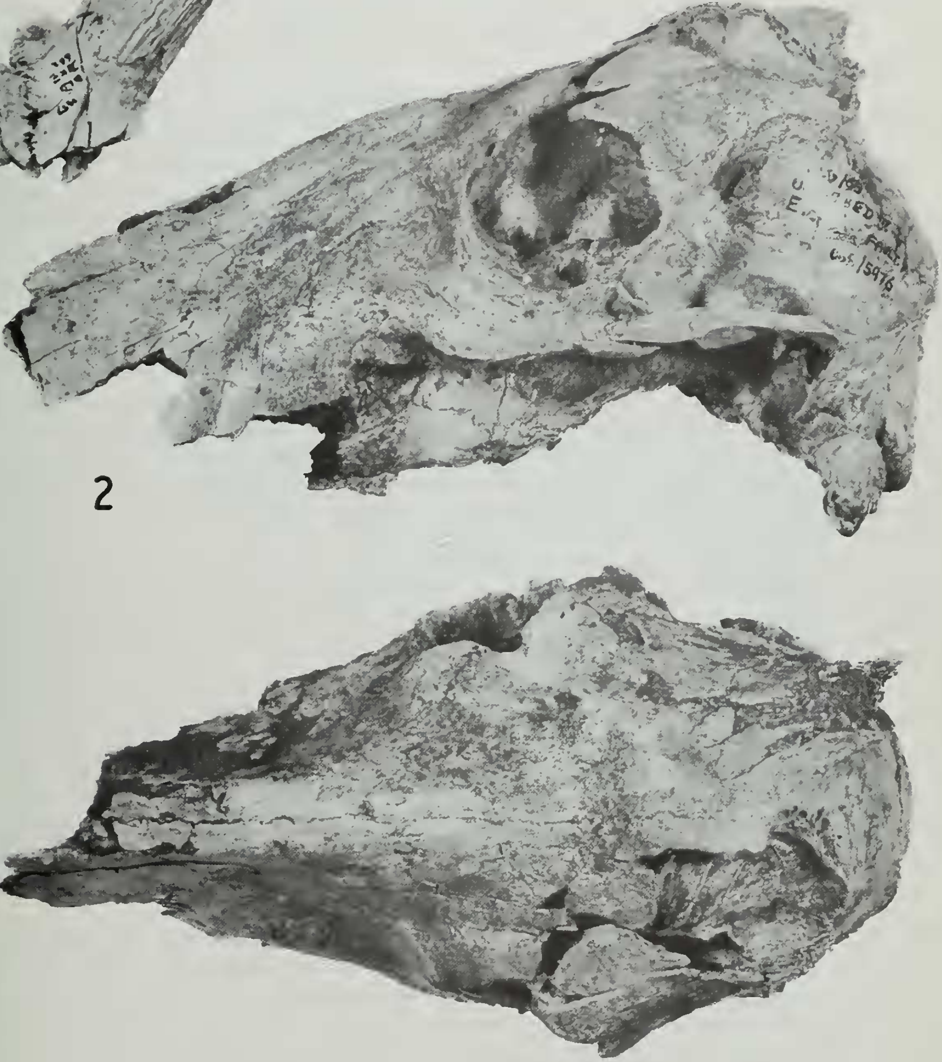


Plate 35 (Upper scale = 50 mm for horn core, lower scale = 50 mm for skull)

Fig. 1 *Aepyceros melampus*. Anterior view of left horn core, BK II 1957.662.

Fig. 2 **Alcelaphini** sp. 1. Lateral and dorsal views of partial skull, 1963.068/5976 from upper Bed IV.

posterolateral keel, transverse ridges, insertions above the back of the orbits, strong divergence from the very base and backward curvature in their lower parts. All this agrees with *B. antiquus*, but the horn cores differ in being short, inserted more obliquely in side view, not having a posterior basal swelling, and showing a much stronger inturning of their tips. This Elandsfontein form has some similarities to the central African populations of *Damaliscus lunatus lunatus*, but has larger and more massive horn cores. We believe that a relationship to *B. antiquus* is more likely.

Genus *AEPYCEROS* Sundevall 1847

TYPE SPECIES. *Aepyceros melampus* (Lichtenstein 1812).

Aepyceros melampus (Lichtenstein 1812)

1965 *Aepyceros* sp. indet. Leakey : 65.

REMARKS. There are a few horn cores of the impala at Olduvai. We have recorded the base of a left horn core THC I 1959.129, an incomplete left horn core with the midfrontal suture BK II 1957.662 (Pl. 35, fig. 1; Leakey 1965 : 65; Gentry 1966 : 104), and the basal part of a left horn core with the midfrontal suture and supraorbital pit BM(NH) M 26926 from the surface of SHK II in 1935. Two pieces of horn core from the surface of Bed II (register) or Bed IV (written on the horn cores), BM(NH) M 14551, are possibly *Aepyceros*.

MEASUREMENTS. Anteroposterior and mediolateral diameters at the base of horn cores of *A. melampus* are:

SHK II surface BM(NH) M 26926	35·7 × 29·3	BK II 1957.662	36·8 × 31·3

COMPARISONS. The occasional occurrence of impala horn cores at Olduvai contrasts with their abundance in the Shungura Formation at Omo. The impala at Omo is sufficiently different from the living one to be taken as a separate, ancestral species, at least until the base of member H. The Olduvai horn cores differ from many of the Omo specimens in being larger, diverging more strongly from the base upwards, and in lacking a posterior keel, and are therefore more like a majority of the living species.

Aepyceros melampus is represented at Peninj by parts of left horn cores A67.232 (WN64.318.CFG.MMG.BSC), A67.246 (WN64.97.MMG.BSC) and A67.255 (WN64.222. TMG(S).USC/MZ), a right mandible with one molar and part of another A67.409 (WN64.312), and possibly other pieces. In the later assemblage of the Kaiso Formation, *Aepyceros* is represented by part of a right horn core M 12592 (Cooke & Coryndon 1970 : 213), a left horn core M 12585, a left upper molar M 12596 and a left M_3 (the last being probably the *Gazella* cf. *wellsi* of Cooke & Coryndon 1970 : 213), all from Kaiso Village. The same authors also record a further horn core from the Nyawiega Early Kaiso assemblage now in the Uganda Museum. Two incomplete Laetolil horn cores in Berlin (Dietrich 1950 : 30, no figure) are labelled '*Aepyceros*' but have no catalogue numbers. The left horn core from Garussi korongo is of a large *Aepyceros*, but the right horn core from Ganeljuio (= Gadjingero by reference to the label for a gazelle maxilla) is less certainly *Aepyceros* and may be conspecific with the horn core of 'Aepycerotinae gen. et sp. indet.' (Dietrich 1950 : pl. 4, fig. 45) discussed on p. 351.

Aepyceros may be present at Makapansgat Limeworks. The morphology of a right mandible BPI M.759 is not sufficiently diagnostic for it to be definitely *Aepyceros* (cf. Wells & Cooke 1956 : 37) and it could be a large specimen of *Gazella vanhoepeni*. The portion of '*Aepyceros* cf. *melampus*' horn core M.654 (Wells & Cooke 1956 : 36, fig. 19) has strong V-shaped transverse ridges on one side and an approach to a keel on the opposite side as in *Aepyceros*, but is very large. However, a large unnumbered right mandible with P_2–M_2 has a small P_4 with the paraconid–metaconid fusion of *Aepyceros* as well as a small P_2, so perhaps a very large *Aepyceros* was indeed present. Some isolated upper molars (right M.43, M.52 and M.763; left M.45, M.49 and M.51) are larger than *G. vanhoepeni* and have strong mesostyles and the posterior lobe less transversely elongated than the anterior one; they also could be of *Aepyceros*.

Indeterminate Alcelaphini

Some alcelaphine fossils at Olduvai are difficult to fit into the general picture.

Species 1. A partial skull 1963.068/5976 from east of the second fault in upper Bed IV or the Masek Beds is well preserved and not crushed but lacks teeth and both horn cores (Pl. 35, fig. 2). The braincase is short and strongly angled on the face and the horn core insertions very oblique in side view, all of which would fit *Parmularius*. However, there is definitely no trace of a parietal boss, and the shallow preorbital fossa occupies a larger area than would be admissible for *Parmularius*. The best suggestion, but not an entirely convincing one, is that this is a member of the *Rabaticeras–Alcelaphus* lineage later than the Bed III fossils and in which there has taken place a decline in size, steepening of the braincase roof, and lowering of the inclination of the horn core insertions.

Measurements on this cranium are:

Skull width across posterior side of orbits	123·0
Width across lateral edges of supraorbital pits	58·6
Length from back of frontals to top of occiput	45·9
Maximum braincase width	77·3
Skull width across mastoids immediately behind external auditory meati	97·6
Occipital height from top of foramen magnum to top of occipital crest	39·4
Width of anterior tuberosities of basioccipital	22·3
Width of posterior tuberosities of basioccipital	27·7

Species 2. A cranium with the basal halves of both horn cores S.208 was collected in 1970 from the Lemuta Tuff Member (Pl. 31, fig. 3; Pl. 32, fig. 1). It has some resemblance to *Rabaticeras arambourgi*, and agrees in size with the JK2 III material of this species. However, it differs in having its horn cores inserted less uprightly in side view and more widely apart in anterior view, and in the frontals between the horn core bases being less raised. Its braincase is low and wide, in contrast to the Elandsfontein cranium of *R. arambourgi*. A partial palate with very worn left M^2 and M^3 was also collected with the cranium; it appears to have root sockets for only two premolars. It is difficult to assess this fossil. One possibility is that it is directly ancestral to *Alcelaphus lichtensteini* rather than to the Bed III *R. arambourgi*. The great width across the braincase and across the horn core insertions are the only basis for this suggestion, while the probable absence of P^2 is a difficulty. The consequent diphylety of *Alcelaphus* would necessitate changes of nomenclature. It is awkward to relate the fossil to *R. arambourgi* if the latter is ancestral to *Alcelaphus buselaphus*, since horn core insertions would first have to become more upright in Bed III times, then more inclined for a second time in the living hartebeest.

Measurements on the cranium S.208 are:

Anteroposterior diameter of horn core at its base	54·7
Lateromedial diameter of horn core at its base	42·2
Minimum width across lateral surfaces of horn core pedicels	128·0
Maximum braincase width	94·4
Occipital height from top of foramen magnum to top of occipital crest	47·5
Width of anterior tuberosities of basioccipital	25·9
Width of posterior tuberosities of basioccipital	33·2

Species 3. Leakey (1965 : 68(c)) referred four horn cores to a category 'cf. Caprini'. These were a left horn core with part of the frontals, orbit and parietal SHK II 1953.280, parts of two other horn cores SHK II surface 1957.92 and SHK II 1953.234, and a right horn core F.3000 with part of the orbit and a good deal of the parietal from the surface of Bed II in 1941 (Pl. 40, figs 1–2). An incomplete frontlet with horn core bases, 1953.067/5460 from BK II East, is likely to be a smaller individual of the same species. The two most complete specimens have horn cores without transverse ridges, inserted rather uprightly and close together on short pedicels above the orbits, hollowed frontals and no parietal boss. All these characters are resemblances to *Rabaticeras arambourgi*, but these horn cores have more mediolateral compression and are nearly straight with only a very slight forward curvature, divergence or torsion. The braincases are as steeply

inclined as in the Bed III and Elandsfontein *Rabaticeras*, and certainly more inclined than in the *Rabaticeras*-like specimen from the Lemuta tuff. Two alternatives seem to be possible for their classification. One, which we favour, is to regard them as a variant within the *R. arambourgi* lineage, and another is to regard them as possibly linked with the 'Villafranchian' *Numidocapra crassicornis* Arambourg (1949 : 290) from Ain Hanech, Algeria. The holotype of this is very large with long horn cores inserted close together on short pedicels above the orbits. The horn cores curve forwards as they rise, nearly parallel to one another, and are probably without transverse ridges or keels. The braincase is strongly bent downwards and has no parietal boss. If the Olduvai horn cores are related to *Numidocapra*, it would be good to know whether they should be classified as Caprinae similar to *Procamptoceras brivatense* Schaub (1923 : 282, figs 1–2) from the Villafranchian of Senèze, France, or as Alcelaphini.

Anteroposterior and mediolateral diameters at the base of the two measurable Olduvai horn cores are:

SHK II 1953.280 52·9 × 39·4 Bed II surface 1941 F.3000 64·6 × 44·1

A frontlet with both horn cores 794 and an almost complete right horn core 839 from Elandsfontein resemble the horn cores SHK II 1953.280 and F.3000 in some characters. They agree in overall size, and in that the horn cores are of normal length, mediolaterally compressed, almost parallel in anterior view, have a clockwise torsion in the right horn core, are without keels or transverse ridges, and with only a very slight or absent postcornual fossa. The midfrontal and parietofrontal sutures are simple and the parietofrontal suture lacks a dorsal indentation centrally. Paired swellings occur in front of the horn cores. The Elandsfontein remains differ from the Olduvai fossils in the more pronounced torsion of the horn cores, their more oblique plane in side view, the lack of any forward curvature, the insertions being possibly wider apart in anterior view and the braincase less steeply angled on the facial axis. It seems unlikely that they have any connection with the Olduvai fossils.

Species 4. A horn core FLKN I 7884 from level 6, a horn core with a crushed braincase FLKN I 5196 P.P.R.10 from level 5 and part of a horn core from Bed I BM(NH) M 14521 could represent a small alcelaphine species (Pl. 40, figs 4–5). The horn cores are very laterally compressed, without keels or transverse ridges, notably long in comparison with their slenderness, and strongly spiralled. However, the first specimen is without its base, and the second is no longer attached to its braincase, so there is no certainty about the planes of insertion or direction of the horn cores' course. A possible fit of the horn core 5196 to its braincase suggests that the horn cores may be inserted obliquely in side view, curving upwards and less backwards from the base. If 5196 were a right horn core its anticlockwise torsion would be the reverse of the situation found in the larger *Rabaticeras*. The hollowed horn core pedicel of 5196, its basioccipital with small localized anterior tuberosities almost as wide apart as the posterior ones, and the very slight development of longitudinal ridges behind the anterior tuberosities could be equally as consistent with membership of the tribe Antilopini or even of the Neotragini as with the Alcelaphini.

Measurements on FLKN I 5196 P.P.R.10 are:

Anteroposterior diameter of horn core at its base	26·8
Mediolateral diameter of horn core at its base	18·7
Width of anterior tuberosities of basioccipital	18·6
Width of posterior tuberosities of basioccipital	22·9

Four small probably alcelaphine mandibles from Olduvai could conceivably belong to the same species as the horn cores, although there is no association between them. They are right FLKN I 1293 from levels 1–2 and left FLKN I 137 from levels 1–3, left F.109 from the surface of Bed I in 1941, and left F.102 from the surface of Bed II in 1941. They have horizontal rami markedly deeper below the molars than below the premolars, paraconid almost fused with the metaconid on P_4, a small P_2, and molars of alcelaphine appearance. Two alcelaphine left mandibles HWK EE 1156 and the more fragmentary 4302 from middle Bed II are also small and deep-jawed, but not so pronouncedly deep under the molars. The paraconid and metaconid are not fused on P_4, and the P_2 had been lost in life.

Measurements on these mandibles are:

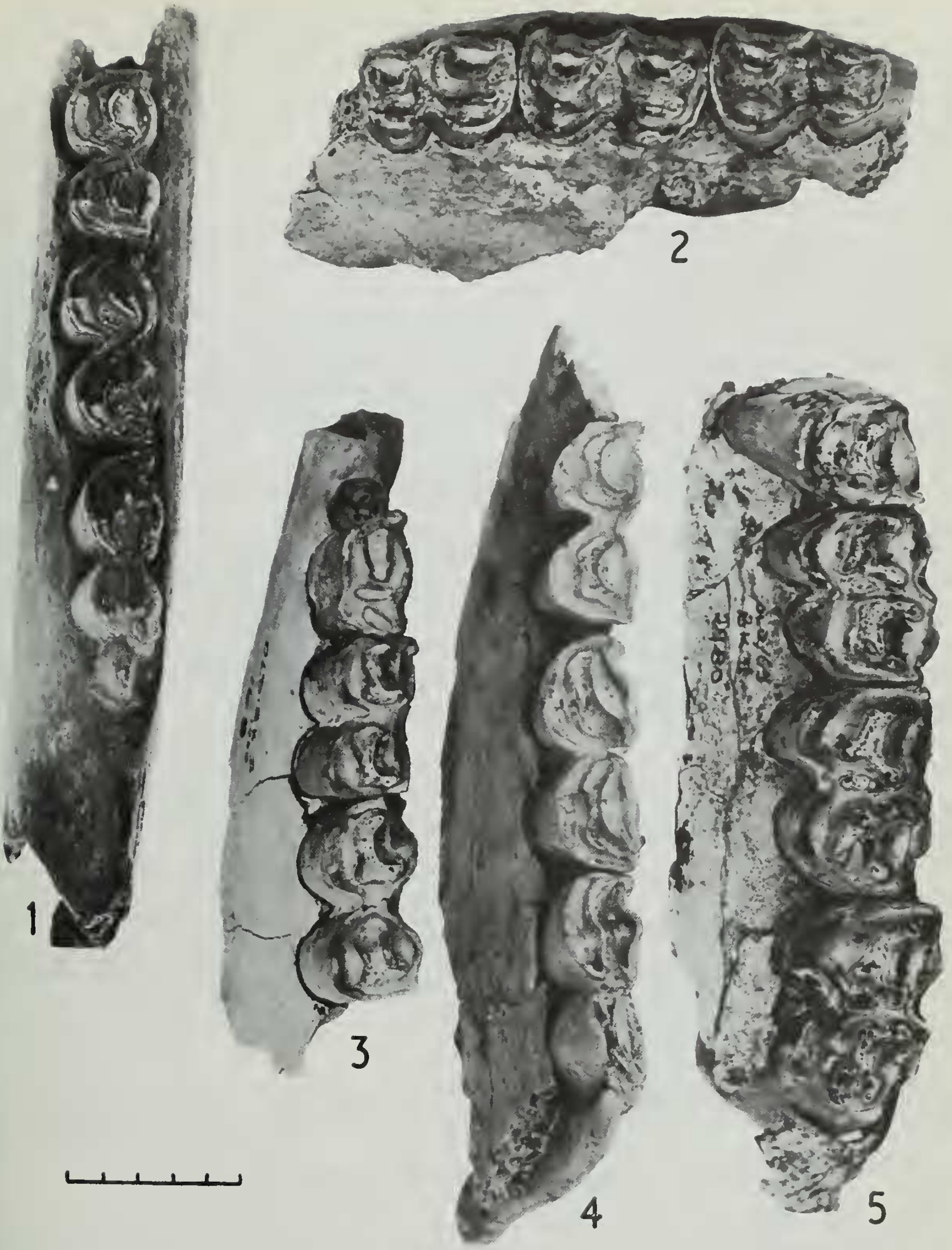


Plate 36 (Scale = 25 mm)

Large alcelaphine dentitions, size group (i).

Fig. 1 Left M_1–M_3, JK2 III A.3261.

Fig. 2 Left M^1–M^3, BK II 1963.670.

Fig. 3 Left P_4–M_2 with root of P_3, BK II 1952.148.

Fig. 4 Left M_1–M_3, MNK II 2070.

Fig. 5 Left P^4–M^3, BK II 1963.2980.

	F.109	F.102	HWK EE 1156
Occlusal length M_1–M_3	50·5	–	46·0
Occlusal length M_2	16·5	–	15·7
Occlusal length M_1	14·4	15·3	13·0
Occlusal length P_2–P_4	–	23·5	11·7 (P_3–P_4)

Limb bones apparently belonging to antilopine-sized alcelaphines are known from DK I, FLKN I, HWK East lower II and HWK EE middle Bed II. They are of a size to be conspecific with the above horn cores and/or mandibles, but there is no direct association. Rather small alcelaphine limb bones continue to occur in later sites, but another possible attribution for these would be to *Damaliscus agelaius*.

The mandibles have some resemblance to the Omo '*Antidorcas* sp.' of Arambourg (1947 : 390; pl. 30, fig. 3) which is not larger than the Olduvai pieces (cf. Gentry 1966 : 67). The Omo mandible agrees best with HWK EE 1156 in its less marked posterior depth, its very short premolar row, and lack of P_2. Further teeth from the Shungura Formation, perhaps of the same unknown species, have been recovered by the American group, e.g. L.465-22 from member F and L.526-4 and L.614-1 from member G.

Measurements of alcelaphine dentitions and limb bones

We cannot identify alcelaphine dentitions from Bed II and Bed III to generic and specific level. All that is possible is to assign the more complete ones to two size classes (Fig. 30; Pls 36, 37). The teeth have a lower level of occlusal complexity than is usual in living alcelaphines. A parallel size system has been set up for limb bones.

Size group (i). According to measurements of the teeth on the neotype skull BM(NH) M 21447 of *Megalotragus kattwinkeli* the largest dentitions belong to this species. The teeth have a simple occlusal pattern. Measurements on two maxillae of this size group are:

	BK II 1963.2980	BK II 1963.458 (immature)
Occlusal length M^1–M^3	89·1	–
Occlusal length M^2	31·0	36·2

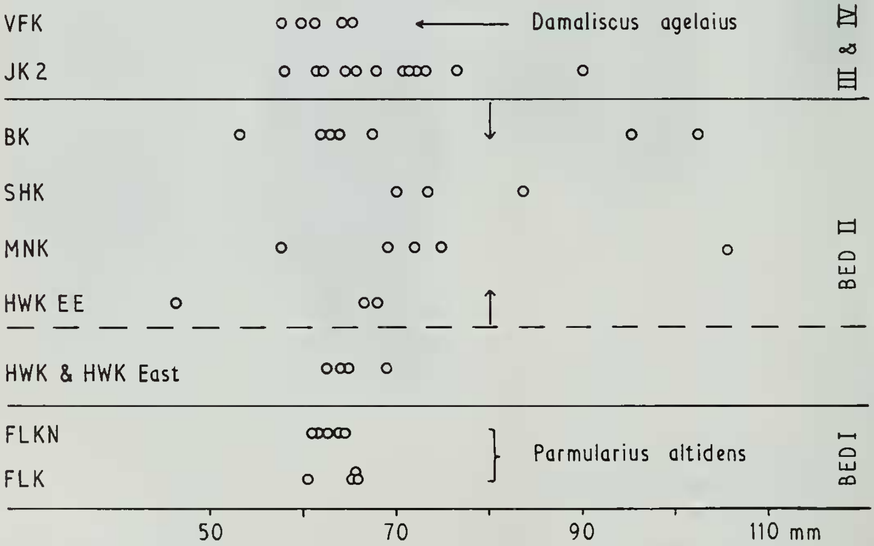


Fig. 30 Length of M_1–M_3 in Olduvai Alcelaphini to show the size classes (i) and (ii) in Bed II. The vertical arrows at 80 mm divide size class (i) from (ii). Earlier and later fossils are shown for comparison. The dashed line demarcates lower Bed II.

Measurements on the more complete mandibles of this size group are:

	MNK II 2070	SHK II 1957.256	SHK II or BK II 068/5536	BK II 1952.622
Occlusal length M_1–M_3	105·7	c. 84·0	90·8	–
Occlusal length M_2	35·2	26·0	–	–
Occlusal length P_3–P_4	–	–	–	31·3

	BK II 1957.713	BK II 1957.979	JK2 III A.2828	JK2 III A.3261
Occlusal length M_1–M_3	102·2	95·3	–	89·9
Occlusal length M_2	30·6	31·1	27·4	29·1
Occlusal length P_3–P_4	–	c. 26·0	–	–

Measurements on the M_2s of nine mandibles from BK II, including two from the mandibles whose measurements are listed above, are:

	Number measured	Mean	Range	Standard deviation	Standard error
Occlusal length M_2	9 (left+right)	28·9	22·2–33·5	3·4	1·15
	5 (left only)	27·3	22·2–31·1	3·7	1·65

A very few dentitions are slightly smaller, but still large, and are probably *Connochaetes taurinus olduvaiensis*. The only measurable one is a maxilla, BK II 1963.670:

Occlusal length M^1–M^3 66·7 Occlusal length M^2 27·5

The largest limb bones belong with these teeth and are presumably *Megalotragus kattwinkeli* and possibly some *Connochaetes taurinus olduvaiensis*. Measurements of length and least thickness are:

Tibiae	BK II Ext 1953.417	360×35·8	BK II 1957.1379	325×34·9
	BK II 1963.2680	374×38·0	BK II 1963.3036	330×30·8
Metatarsals	MNK II 169	300×26·8	MNK II 2718	273×20·7
	SHK II 1957.231	288×24·2	SHK II 1957.839	271×24·1
	SHK II 1967.731 (immature)	261× –	BK II 1953.067/5508	290×26·1
	BK II Ext 1953.416	311×28·6		
Radii	SHK II 1957.283	337×35·4	BK II Ext 1953.426+428	317×34·6
	BK II 1963.854+863	307×40·1		
Metacarpals	MNK II 2704	257×30·7	SHK II 1957.558	237×27·4
	SHK II 1957.1350	247×28·6	BK II 1952.219	242×33·3
	BK II 1963.2609	264×26·9	JK2 III A.1272	263×22·1

Two metatarsals in this size group are shorter than those listed above and have low and wide distal condyles. They are probably *Connochaetes taurinus olduvaiensis*. Measurements of their length and least thickness are:

MNK II 752 239×25·0 BK II 1953.067/5509 249×29·2

Size group (ii). Dentitions and limb bones smaller than those of the above group are probably of *Parmularius angusticornis* and *Damaliscus niro* but may include some *Connochaetes*. The teeth are about the size of living *Alcelaphus buselaphus* and slightly larger than Bed I *Parmularius altidens*. Measurements on mandibles in this size group are:

	MNK II 136	MNK II 976	MNK II 2403	SHK II 1957.268	SHK II 1957.455
Occlusal length M_1–M_3	69·3	72·4	75·0	70·3	73·5
Occlusal length M_2	23·5	22·5	23·0	22·6	24·5
Occlusal length P_2–P_4	21·5	–	–	–	–

	BK II 1963.24	BK II 1963.941	BK II 1963.1065	BK II 1963.1442
Occlusal length M_1–M_3	63·9	67·6	–	c. 62·0
Occlusal length M_2	20·2	23·1	21·4	20·5
Occlusal length P_2–P_4	–	–	c. 23·0	–

	BK II Ext 1953.76	JK2 III A.1444	JK2 III A.2060	JK2 III A.2091
Occlusal length M_1–M_3	63·0	76·7	75·8	–
Occlusal length M_2	22·0	24·2	23·8	20·5
Occlusal length P_3–P_4 (P_2 missing)	–	–	–	22·7

	JK2 III A.2780	JK2 III A.2934	JK2 III A.3012
Occlusal length M_1–M_3	72·3	64·5	72·9
Occlusal length M_2	22·7	19·5	24·2
Occlusal length P_2–P_4	–	c. 31·4	–

	JK2 III B.FQ4-10	JK2 III B.FQB-1	JK2 III B.FL2-21	JK2 GP8 III GN 16
Occlusal length M_1–M_3	71·0	71·2	–	65·3
Occlusal length M_2	22·9	23·6	25·8	20·2
Occlusal length P_2–P_4	11·2	–	–	–

Immature mandibles BK II 1963.291, BK II 1963.2550 and JK2 III A.2157 have deciduous P_2–P_4 measuring 38·0, 37·1 and 40·3. BK II 1963.067/1635 has deciduous P_3–P_4 (deciduous P_2 was missing in life) measuring 27·6 mm.

Measurements on the M_2s of 10 mandibles from BK II, including five from the mandibles whose measurements are listed above, are:

	Number measured	Mean	Range	Standard deviation	Standard error
Occlusal length M_2	10 (left+right)	20·4	16·5–23·1	1·7	0·55
	6 (left only)	20·2	16·5–23·1	2·3	0·93

Measurements of length and least thickness of the limb bones in this size group are:

Tibiae	MNK II 167	333 × 29·5	JK2 GP8 III GN 22	310 × 22·3
Metatarsals	SHK II 1957.933	234 × 17·9	JK2 III A.1671	271 × 17·2
Radii	SHK II 1957.209	262 × 30·1	BK II 1957.26	244 × 27·0
	JK2 III A.1305+1491	264 × 26·1		
Metacarpals	SHK II 1957.208 (immature)	218 × 17·1	SHK II 1957.330	220 × 18·8
	BK II 1957.1381	227 × 20·3	BK II 1963.3229	224 × 18·4
	JK2 III A.1592	224 × 18·8		

Associated femur BK II Ext 1953.067/5364 259 × 25·9, tibia BK II Ext 1953.067/5363 319 × 25·9 and metatarsal BK II Ext 1953.067/5506 246 × 19·3.

Plate 37 (Scale = 25 mm)

Alcelaphine dentitions, size group (ii).

Fig. 1 Left P_4–M_3, SHK II 1957.268.

Fig. 2 Left M_1–M_3, BK II 1963.941.

Fig. 3 Left P_3–M_3, JK2 III 068/6692.

Fig. 4 Right P_3–M_3 with socket for P_2, JK2 III A.2934.

Fig. 5 ***Parmularius altidens*.** Left P^3–M^3, FLKN I 1136. Same scale as above.

Fig. 6 **Alcelaphini** indet. Lateral view of left mandible, HWK East II 168. For this illustration the scale = 50 mm.

1

2

3

4

The smallest dentitions and limb bones of this size group are likely to belong to a smaller alcelaphine than *Parmularius angusticornis* or *Damaliscus niro*, possibly *D. agelaius*. We cannot separate clearly a third size group, but included here would be a maxilla, MNK Skull Site 89:

Occlusal length M^1–M^3 52·9 Occlusal length M^2 18·9

Measurements on the smallest of the mandibles in this size group are:

	MNK II 1725	BK II 1957.21	BK II 1957.1452	JK2 III B.FFM3-14
Occlusal length M_1–M_3	*c.* 57·7	–	53·2	–
Occlusal length M_2	17·4	19·5	16·5	19·0
Occlusal length P_2–P_4	–	–	18·7	–

	JK2 III A.384	JK2 III A.1372	JK2 III 068/6692	JK2 GP8 III Sec 6
Occlusal length M_1–M_3	–	58·0	62·0	61·9
Occlusal length M_2	–	19·3	20·5	20·1
Occlusal length P_3–P_4	20·4	–	23·9	–

Measurements on the smallest of the limb bones in this size group are:

Tibia	BK II 1957.1261	243 × 18·0		
Metacarpals	BK II Ext 1953.337	202 × 18·0	BK II 1963.2311	191 × 17·8
	JK2 GP8 III GN	193 × 17·8		

Tribe NEOTRAGINI

At the present day this tribe consists of 14 species of small antelopes. Their horn cores are sometimes short and always of small cross-sectional area, not very compressed, inserted widely apart and above the back of the orbits, straight or curved slightly forwards but not backwards, not very divergent and occur nearly always only in males. The midfrontal and parietofrontal sutures are not very complicated, the braincase is little angled on the facial axis but its back part is often downturned, supraorbital pits are small and a preorbital fossa is present. There are generally no basal pillars on the molars, there are no outwardly bowed ribs between the styles on the lateral walls of the upper molars, the enamel outer walls of the molars tend to be straight and with pointed rather than rounded corners.

The genera in the tribe are:

Neotragus H. Smith 1827 (including *Nesotragus*), with three living species,
Madoqua Ogilby 1837 (including *Rhynchotragus*), with five living species,
Oreotragus A. Smith 1834, with one living species,
Dorcatragus Noack 1894, with one living species,
Raphicerus H. Smith 1827, with three living species,
Ourebia Laurillard 1841, with one living species.

Ourebia has a number of reduncine-like characters and is possibly not of this tribe. *Pelea* may have to be included in the Neotragini, unless the single species, *P. capreolus* the Vaal rhebok, should turn out to belong in the Antilopini (Oboussier 1970) or in the Caprinae. So few neotragine fossils have been found that a fuller discussion of the tribe is unnecessary.

A pair of Olduvai horn cores with a small part of the frontal FLKN I 10229 are small enough to belong to a neotragine species (Pl. 40, fig. 3). They are too incomplete for definite orientation, but what appear to be the front edges may be less concave in side view than in living neotragines. *Raphicerus* would have been a reasonable attribution, except that sinuses are present in the frontals. These throw doubt on the horn cores being neotragine at all.

An incomplete right mandible FC West II 167 with deciduous P_2–P_4 is extremely small and probably neotragine.

The Olduvai scapula called *Nesotragus moschatus* subsp. by Schwarz (1937 : 40) was destroyed in Munich during the Second World War.

OTHER FOSSIL NEOTRAGINES. A number of Laetolil horn cores in Nairobi (left 1959.107 and 1959.570, right 1959.222, 1959.472 and 1959.571) can be referred to *Madoqua* by their oblique insertions, medial keels and slightly less marked lateral keels. 1959.570 is rather larger than the others. They agree with the Berlin horn cores of *Praemadoqua avifluminis* Dietrich (1950 : 34; pl. 1, figs 3–4). We saw twelve such horn cores in Berlin.

Several Laetolil dentitions and isolated teeth are also referable to *Madoqua* on their overall size. In Nairobi there are left maxilla 280, right maxilla 163 + 164, two right upper molars numbered 165, left mandibles 58, 70, 115, 156, 157, 159, 160 + 161, 297, 300 + 301, 307, 449, 604, 607 + 612 and 613, right mandibles 154, 155, 278, 295, 305, 448, 450, 451, 606, 608, 610 + 611, and immature right mandibles 158 and 306 which were all found in 1959. In London there are left mandibular pieces BM(NH) M 15107 and M 15108, right mandibles M 15109, M 15111, M 26782, M 26783 and immature left mandible M 26781. The premolar row length, as deduced from 154, 278, 297, 307, 607 + 612 and 610 + 611, has a similar proportion to the molar row length as in extant *Madoqua*. The very small back lobe of the M_3s, in all except M 15109, agrees with the subgenus *Rhynchotragus* within *Madoqua* and not with the subgenus *Madoqua* s. s. in which the lobe has completely gone. The lobe is absent in M 15109. These dentitions agree with those assigned to *Praemadoqua avifluminis* by Dietrich (1950 : 34; pl. 3, figs 25–26, the M_3 of fig. 25 being an odd tooth which has been stuck to the rest).

A complete right metatarsal 1959.218, from Laetolil and now in Nairobi, has a length of 94·5 and least thickness of 7·3. It is slightly shorter and relatively thicker than living *Madoqua* (Fig. 31), but otherwise is about the right size and with appropriate morphology. It differs from the suni *Neotragus moschatus* in its greater size and length and in the more upright outer anterior edges of the distal condyles, the larger ectocuneiform facet at the proximal end, the less marked flange medially at the top of the posterior side, and the absence of two foramina at the top of the posterior side. It is too large for the other (i.e. not east African) species of *Neotragus*, too small for *Raphicerus*, *Dorcatragus* and *Ourebia*, and not short enough for *Oreotragus*. The two duiker genera *Cephalophus* and *Sylvicapra* can be eliminated because there is no longitudinal groove on the anterior surface.

Two right mandibular pieces from Laetolil in Nairobi 1959.153 and 1959.447, the left mandible BM(NH) M 26778 and perhaps the left M_3 M 26779 are larger than the mandibles of contemporaneous *Madoqua* and about the size of *Raphicerus*. The P_4s on 1959.447 and M 26778 are unlike *Ourebia* and quite similar to *Raphicerus*. The molars of M 26778 retain basal pillars.

Fig. 31 Proportions of *Madoqua* metatarsals.
X = living east African *M. kirki*, O = Laetolil metatarsal 1959.218, assumed to be conspecific with the *Madoqua* fossil horn cores from that area.

The mandibles agree in size and morphology with those assigned by Dietrich (1950: 25; pl. 2, fig. 13) to the smallest of his three gazelle species, *Gazella hennigi*, but they are too small for a gazelle.

A right upper molar, BM(NH) M 25708 from Kanjera, is probably of *Ourebia*.

A horn core, a mandible and the distal end of a metatarsal represent the Neotragini in members E, F and G of the Shungura Formation, Omo.

A couple of crania, some frontlets and horn cores and many dentitions from Elandsfontein are of *Raphicerus*. They represent a larger antelope than the living steinbok or grysbok, their supraorbital pits are not obscured by overgrowth of the frontals, the horn cores are set more obliquely in side view, and a few of the larger horn cores tend to have a posterolateral keel. The horn cores on one frontlet, 14153, have a mid-lateral keel as well and resemble some neotragine horn cores from Langebaanweg. The Langebaanweg material, consisting of a right horn core and associated right maxilla both numbered L.12238 and several other horn cores and dentitions, seems likely to be an early *Raphicerus*. The horn cores still have a more irregular cross-section than those at Elandsfontein and they show a posterolateral keel, a tendency to an anterolateral longitudinal concavity and other irregular keels or ridges. They are also larger as a whole. The Elandsfontein and Langebaanweg material make it clear that living *Raphicerus* has evolved from ancestors with larger and obliquely inserted horn cores. Further fossils of *Raphicerus* coming to light in east Africa will have to be compared with this South African material. The size diminution in the history of *Raphicerus* contrasts with the size stability of the Laetolil fossil *Madoqua*.

There are some other *Raphicerus* fossils in South Africa. Horn cores from Baard's quarry at Langebaanweg are smaller than at Elandsfontein, and cranial remains from the late sites of Melkbos (Hendey 1968 : 111) and Swartklip (Hendey & Hendey 1968 : 61) are indistinguishable from living *Raphicerus*. A right horn core BPI M.478 from Makapansgat Limeworks is like those at E quarry Langebaanweg, and was published as *Cephalophus pricei* (Wells & Cooke 1956 : 12, fig. 6). The tooth rows assigned by the same authors to *C. pricei*, one of which is the holotype, are from a bushbuck-sized tragelaphine.

A frontlet BPI M.476 of a supposed *Oreotragus* and some small dentitions from Makapansgat Limeworks were referred to *O. major* by Wells & Cooke (1956 : 35, figs 17–18). This name had been founded by Wells (1951 : 167, fig. 1) on a large *Oreotragus* skull with palate BPI M.651 from a red breccia deposit of unknown age in the Makapan valley. The Limeworks frontlet has very short horn cores with some degree of anteroposterior compression, and is not very like the *O. major* holotype. The Limeworks dentitions have premolar rows which were probably slightly longer relative to the molar rows than in the living klipspringer *O. oreotragus*. The frontlet M.476 differs from the Makapansgat *Raphicerus* horn core M.478 by its shortness, more upright insertion and a more regular shape of cross-section.

Tribe **ANTILOPINI**

Living members of the Antilopini are the springbok, gerenuk, dibatag, several species of gazelle and the Indian blackbuck which has spiralled horns. They are small to medium-sized, long-legged, grazing or browsing antelopes often adapted to life in arid areas. The skulls are not very distinctive at tribal level, especially when fossil forms are taken into account. The main skull features are: horn cores inserted above or partly behind the orbits, horns not always absent in females, face and braincase moderately long, braincase little angled on the facial axis, parietofrontals' suture complicated, preorbital fossae present, mastoids large, basioccipital moderately long and not narrowing anteriorly except in some early forms, premaxillae large and long, infraorbital foramen above P^2 or P^3, teeth of early forms brachyodont and with basal pillars but becoming hypsodont and losing basal pillars during evolution, central cavities with a simple outline, P_4s without fusion of paraconid and metaconid to form a complete medial wall anteriorly except in some east Asian gazelles.

Gazella Blainville 1816 is an exceptional genus among bovids in spanning both the Palaearctic and Ethiopian faunal realms. At present it occurs no further south in Africa than central Tanzania.

The species may be grouped as follows:

1. An east Asian group of two or three species frequently placed in the subgenus *Procapra*. Related to them is the Persian gazelle *Gazella subgutturosa*.

2. A second main Palaearctic group comprises the various gazelles of Arabia and the Near East, *G. bennetti* extending into India, and the widespread *G. dorcas* (Linnaeus 1758) of north Africa which includes *G. dorcas pelzelni* Kohl 1886, of the northern Somalia coastal plain. This whole group is likely to form one or two species.

2a. Possibly related to group 2 are *G. cuvieri* (Ogilby 1841) of the Atlas region, *G. leptoceros* (F. Cuvier 1842) of sandy areas of the Sahara and *G. spekei* Blyth 1863 of Somalia.

3. The west African *G. rufifrons* Gray 1846 and *G. thomsoni* Günther 1884 seem to be a truly Ethiopian group slightly larger than *G. dorcas* and with a different skull morphology. Despite the skull similarities between the two species, *G. rufifrons* has a longer premolar row than *G. thomsoni*.

4. A second Ethiopian group is constituted by the three large species *G. dama* (Pallas 1766) of west Africa, *G. soemmerringi* (Cretzschmar 1826) of Somalia and the Sudan, and *G. granti* Brooke 1872 of east Africa.

We might therefore expect to find at Olduvai relatives of groups 3 and 4, but we should regard it as a matter of note if gazelles closely related to group 2 were found. In fact the Olduvai gazelle is rather poorly known, but does seem to be related to group 3.

Antidorcas Sundevall 1847 is a genus of which the South African springbok *A. marsupialis* (Zimmermann 1780) is the only living species. Living springbok females are bigger-horned than gazelle females, and though the horns of springbok females are mostly less bent backwards than in the males, Lange (1970 : 73) found sexual dimorphism in the skulls of springbok to be less than in gazelles.

Litocranius walleri (Brooke 1878) and *Ammodorcas clarkei* (O. Thomas 1891), the African gerenuk and dibatag, do not occur at Olduvai. Leakey (*in* Clark 1959 : 230) identified some limb bones from Broken Hill, Zambia, as *Litocranius*, but some skull parts would be preferable for a definite identification (see p. 436).

Antilope cervicapra (Linnaeus 1758) the Indian blackbuck is the final living antilopine. It is not known from Olduvai but a pair of *Antilope* horn cores has been found below tuff D of the Shungura Formation at Omo.

As a result of the study of material excavated at Olduvai since 1960 there can be considerable modification to the history of the Antilopini in east Africa described by Gentry (1966), although the central conclusion still stands that most of the east African fossils of this tribe are related to *Antidorcas*, now confined to Namibia (South West Africa), South Africa and eastern Botswana, rather than to *Gazella*. From specimens of Antilopini teeth excavated since 1960, especially those in early stages of wear, it now appears that there is only one species of springbok-like antelope in Bed I (cf. Gentry 1966 : 77). Indeed, the amount of variation in horn cores and the levels of occurrence of different varieties suggest that all the Olduvai material, except for one frontlet, is of one species for which the name used hitherto has been *Phenacotragus recki*.

Antilopini have been found at most South African fossil sites. Among them is '*Phenacotragus*' *vanhoepeni* Wells & Cooke (1956 : 43, pls 22–24) known only from Makapansgat Limeworks and now thought to be referable to *Gazella* (Wells 1969b : 162). We concur with Professor Wells' opinion. With this awkward species no longer congeneric with the east African type species of *Phenacotragus*, there seems to be no reason for not sinking the latter genus in *Antidorcas* (cf. Gentry 1966 : 97). This will now be done.

Genus *ANTIDORCAS* Sundevall 1847

1937 *Phenacotragus* Schwarz : 53.

TYPE SPECIES. *Antidorcas marsupialis* (Zimmermann 1780).

GENERIC DIAGNOSIS. Small to moderate-sized antelopes; horn cores of males not usually very compressed, often with transverse ridges, generally diverging strongly from the base or in their distal parts, usually bending backwards a short distance above the base, often more massive basally in relation to their length than in gazelles; frontals hollowed internally and at a higher level between the horn core bases than at the orbital rims; parietofrontals' suture not always complicated; braincase rather short; supraorbital pits small; nasals long; basioccipital with well-marked anterior tuberosities on which the surface rugosity tends to be confined to the anterolateral parts, and with a rather flat appearance of the whole bone behind the anterior tuberosities; upper molars with stronger styles than in *Gazella*; M_3s with a well-developed rearmost (third) lobe; premolar rows shorter than in *Gazella*, with P_2s reduced or absent; mandibular ramus often markedly deepened under the molars.

This genus contains four species in our opinion:

Antidorcas marsupialis, the living springbok,
A. recki (Schwarz 1932), extinct,
A. bondi (Cooke & Wells 1951), extinct,
A. australis Hendey & Hendey 1968, extinct.

Antidorcas recki (Schwarz 1932)

1932 *Adenota recki* Schwarz : 1; pls 1–2.
1937 *Phenacotragus recki* Schwarz : 53; pl. 1, fig. 1.
1949 *Gazella wellsi* Cooke : 38, fig. 11.
1965 'Other gazelles' Leakey : 64(a), (b), (c), (d), (g), (h), (i), HWK II 473 of (j), pls 83–85. Specimens (e) and (k) are indeterminable as no catalogue numbers are given.
1965 *Phenacotragus recki* Leakey : 65; pl. 87.
1965 Reduncini indet. Leakey : 47; pl. 53.
1966 *Gazella wellsi* Gentry : 56; pls 1, 2A and B.
1966 'Other gazelles' Gentry : 64 group A; KK I 1959.309 of pl. 2C.
1966 *Phenacotragus recki* Gentry : 77; pls 5–8.

Diagnosis. A species of *Antidorcas* differing from living *A. marsupialis* in its smaller size; horn cores more mediolaterally compressed and often more sharply bent backwards in their distal parts; ethmoidal fissure present; preorbital fossae less deep posteriorly and possibly larger; basioccipital narrower; teeth smaller; premolar rows less reduced but P_2 sometimes absent at least in later life; upper molars with more concave lateral walls behind the mesostyle; radii, tibiae and metapodials shorter, tibiae with more forward curvature, radii with smaller lateral tubercles proximally. Some populations are without increased divergence of the more distal parts of the horn cores.

Holotype. A skull with dentitions and the right horn core from Olduvai, formerly in Munich but unfortunately destroyed during the Second World War. A cast of this skull is in London, BM(NH) M 21460, and a cast of the cast is in the Nairobi collections.

Horizon. According to Dietrich (1933 : 301) the holotype skull came from 'Horizont 4?'. The species is known by numerous horn cores and dentitions from Bed I to Bed IV at Olduvai, and occurs at Kanjera, Peninj, Laetolil and the Omo Shungura Formation. In South Africa it is known from Bolt's Farm, Elandsfontein and the Vaal River gravels.

Remarks. Remains of *A. recki* in London are a herd excavated from SHK II in 1935 consisting of at least eleven mostly immature individuals (Gentry 1966 : 77); a right horn core M 22360 from DK I in 1935; left horn core M 14513 from Bed I in 1931; right horn core M 14509 from Bed I in 1931; cranium with the bases of both horn cores M 22365 from VEK I; two right horn cores, M 14510 and M 14512, found in Bed I in 1931; left horn core M 14511 from Bed I in 1931; right horn core M 22363 from Bed I in 1947; base of a left horn core M 22479 from Bed I; left horn core M 21457 from VEK I in 1935, the 'Mongolian gazelle' (Leakey 1965 : 64(b)), considered as possibly a small *Damaliscus* or related genus by Gentry (1966 : 104); left horn core M 21456 found on the surface of VEK II in 1935; distal half of a left horn core M 22361 from VEK II in 1935; cranium with horn cores M 21463 from the surface of FLK II in 1935 (Leakey 1965 : 64(d), pl. 85, which is not M 21462 from VEK I in 1931 as stated); left female horn core

M 22362 from FLK II in 1935; the medial basal part of a right horn core M 14565 from Bed IV in 1931; right horn core M 14563 from VEK IV.

Characters of the face of *A. recki* are known from the cast of the holotype skull and partly from the two Nairobi specimens FLKN I 6334 and FLKN I 7266 (Pl. 39, fig. 4). The small frontlet with horn core bases in Nairobi, FLKN I 1039, figured as Reduncini indet. by Leakey (1965 : 47, pl. 53), is here identified as *A. recki.*

Most horn cores of this species from Bed I agree well with *Gazella wellsi* Cooke, according to an unpublished paper by Dr H. B. S. Cooke on the South African Bolt's Farm site in which he deals with specimens more complete than the holotype mandible from the Vaal River gravels and supposedly conspecific with it. *G. wellsi*, as there understood, is characterized by horn cores that are bent back sharply near the base, fairly strongly divergent from the base in anterior view but without sharp outward divergence of the distal part, with a flattened lateral surface, little transverse compression, a tendency to a posterolateral edge and well-marked transverse ridges on the anterior surface.

The London herd was referred to *Phenacotragus recki* Schwarz by Gentry (1966 : 77). The barely adult cranium BM(NH) M 21464 (Leakey 1965 : pl. 83; Gentry 1966 : pl. 5A–B) and older frontlet M 21462 (Leakey 1965 : pl. 84 which is not M 21463 as stated in the caption; Gentry 1966 : pl. 5C–D) have horn cores which differ from those in Bed I by being longer, more nearly parallel at the base in anterior view and then diverging more in their distal parts, more symmetrical in cross-section and without a flattened lateral surface. The horn cores of the London cast of the *P. recki* holotype, M 21460, agree in these features except that they are less nearly parallel at the base and rise further before bending backwards.

The extensive variation among *A. recki* horn cores weakens any simple concept of different horn core types in successive horizons at Olduvai. Besides the commonest sort of Bed I '*Gazella wellsi*' horn core already described, there are at least four other sorts from horizons below the Lemuta Tuff. One, represented by horn cores KK I 1959.309, BM(NH) M 14512 from Bed I, HWK II 1959.472, HWK EE II 1972.2780 and HWK EE II 1972.3108 differs by being more strongly compressed and having a less clearly flattened lateral surface. The HWK II horn core is much smaller than the others and might be a female or perhaps a small male. Another variety, represented by horn core 1960.067/250 from FLKN I level 5 is more divergent distally, has less pronounced backward bending and is definitely without a flattened lateral surface. Yet another, represented by horn cores FLKN I 8659 from levels 1 to 2 and FLKN I 8194 from level 5 (which is associated with antilopine postcranial bones), has strong mediolateral compression, an almost regular oval cross-section and an evenly increasing degree of backward curvature in side view. A fourth sort, represented by horn core BM(NH) M 22360 from DK I in 1935, is narrowed anteriorly but this is only a small difference. We do not know that the sort of horn core which happens to have become most commonly fossilized in these horizons at Olduvai is more typical of the species than the other varieties. Horn cores with many Bed I '*Gazella wellsi*' features may come from deposits later than the Lemuta Tuff, examples being the horn core BM(NH) M 14563 supposedly from Bed IV, and probably the Bolt's Farm material. These later horn cores are our main reason for not founding two chronological subspecies for those *A. recki* specimens occurring before and after the Lemuta Tuff. Also, the horn cores BK II 1955.71 and BM(NH) M 14513 from Bed I at Olduvai, BM(NH) M 15862 from Kanjera, A67.256 and A67.257 (WN64.113) from Peninj constitute yet another (mainly later than Bed I) morphological variety within *A. recki*; they are short and taper rapidly to a point from their thick bases, and have no flattened lateral surface or transverse ridges. Horn cores from other sites in Africa may well show still further variations in morphology. In these circumstances all we can say is that the majority of Olduvai Bed I and lower Bed II horn cores show no distal divergence, but most of those from later levels do.

The question of which horn cores, if any, represent the females of *A. recki* is still unsolved. The former concept of Gentry (1966 : 79) about possible female horn cores cannot be maintained. It is now certain that variation among the Olduvai horn cores is too complicated to permit the clear separation of two sexual types. A possible female would be BM(NH) M 22362, erroneously taken by Gentry (1966 : 65, pl. 7A) as a female of the Olduvai *Gazella* species. The horn core

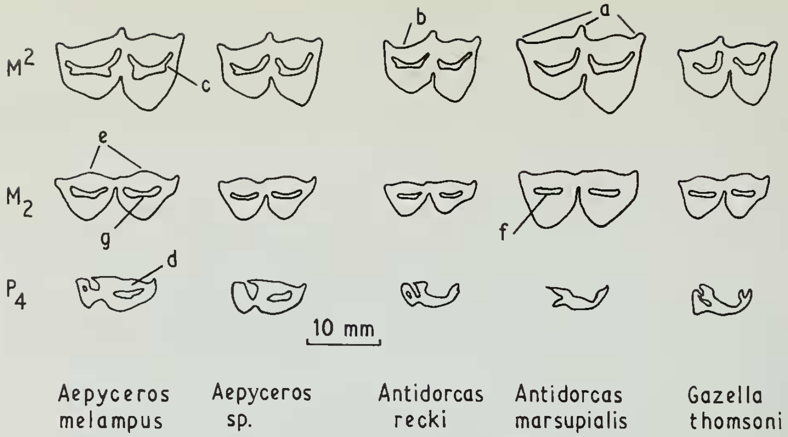


Fig. 32 Occlusal views of teeth of *Aepyceros* and Antilopini. All teeth are of the right side, and the anterior direction lies to the right. *Aepyceros* sp. is from the Shungura Formation, members B to G.

pedicel is hollowed, which fits *Antidorcas*, and there is very little backward bending. The only acceptable alternative to M 22362 as a female is to assign the more slender but otherwise normal horn cores, for example FLKN I 6334 and HWK II 1959.472, to the female sex. At present we are undecided which is the correct solution.

As a result of seeing South African fossil antilopine material and the abundant earlier impala from Omo, we can revise the list of tooth differences given by Gentry (1966 : 96) for distinguishing *Antidorcas* teeth from those of *Gazella* and *Aepyceros* (Fig. 32, a–f):

1. The styles on upper molars are strong in living and fossil *Antidorcas* and *Aepyceros*; they are less pronounced in living *Gazella*, but the Makapansgat Limeworks *G. vanhoepeni* does not differ appreciably from *Antidorcas* (a).
2. A concave posterior part of the lateral wall of upper molars is frequent in fossil *Antidorcas*, *G. vanhoepeni* and living and fossil *Aepyceros*; this is linked with the strength of the mesostyle and therefore with the previous character (b).
3. A tendency to complicated central cavities is found in living and fossil *Aepyceros* upper molars (c).
4. Paraconid–metaconid fusion to close the anterior part of the medial wall of P_4 occurs only in *Aepyceros* (d).
5. There is possibly more outward bowing of the medial walls of lower molars of living *Aepyceros* (e).
6. Central cavities on the lower molars become straight late in wear in *Antidorcas* and some *Gazella*; in *Aepyceros* they often appear constricted centrally and straightening does not occur in late wear (f).
7. M_3 may be relatively longer in later wear in *Antidorcas*.
8. Premolar reduction is carried further in *Antidorcas* than in *Gazella* and *Aepyceros*. It is especially pronounced in *Antidorcas marsupialis*.
9. Deepening of the horizontal ramus beneath the molars is noticeable in most *Antidorcas* (but not, for example, in the majority from Olduvai Bed 1).

Thus the differences between the fossil teeth of *Antidorcas* and *Gazella* are few, and at a time level such as the Shungura Formation of Omo it is hard even to distinguish *Aepyceros* teeth.

A large number of limb bones of *Antidorcas recki* have been excavated from Bed I, Olduvai. The tibiae, radii and metapodials are shorter and thicker than in living Antilopini, and there is no sign of the very long metatarsals characteristic of living springbok (Fig. 33).

MEASUREMENTS. Measurements on the crania of *A. recki* are:

	VEK I M 22365	SHK II M 21464	FLK II M 21463	M 21460 (cast)
Skull width across posterior side of orbits	–	85.2	–	94·6
Length of horn core along its front edge	–	129·0	–	–
Anteroposterior diameter of horn core at its base	–	30·6	29·5	37·4
Mediolateral diameter of horn core at its base	–	24·6	24·0	30·7
Minimum width across lateral surfaces of horn core pedicels	–	59·0	65·8	–
Width across lateral edges of supraorbital pits	–	30·6	33·4	30·2
Length from back of frontals to top of occiput	63.3	59·8	–	–
Length from midfrontal suture at the level of the supraorbital pits to top of occiput	95·3	93·2	–	97·6
Maximum braincase width	–	*c.* 51·7	–	64·5
Skull width at mastoids immediately behind external auditory meati	–	57·1	–	73·3
Occipital height from top of foramen magnum to top of occipital crest	–	22·9	–	–
Width of anterior tuberosities of basioccipital	23·4	17·0	–	–
Width of posterior tuberosities of basioccipital	29·0	23·2	–	–
Occlusal length P^2–P^4	–	–	–	23·3

Measurements on two frontlets of *A. recki* are:

	FLKN I 1039	SHK II M 21462
Skull width across posterior side of orbits	101·0	92·0
Length of horn core along its front edge	–	*c.* 177·0
Anteroposterior diameter of horn core at its base	35·2	33·8

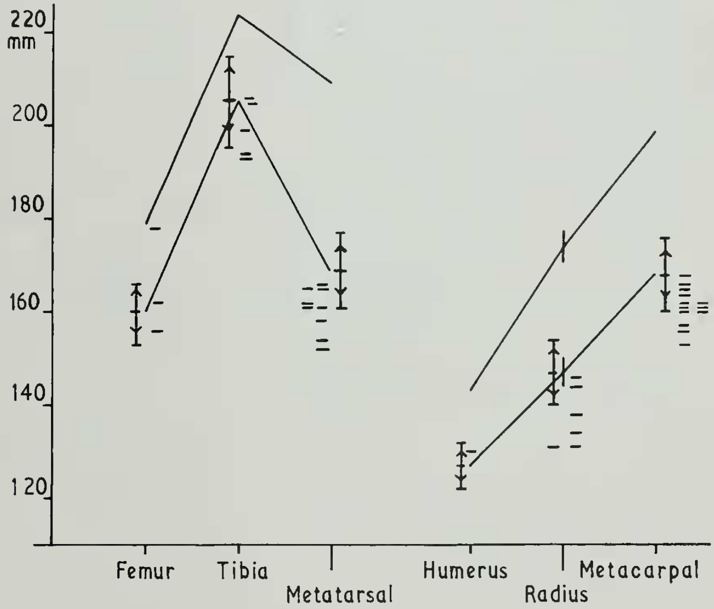


Fig. 33 Lengths of limb bones in Antilopini. The upper line is the mean of 6 *Antidorcas marsupialis*, and the lower of 14 *Gazella thomsoni*. Ranges and standard deviations have been added for the latter. Horizontal dashes indicate antilopines from Bed I, Olduvai Gorge.

Mediolateral diameter of horn core at its base	27·2	25·6
Minimum width across lateral surfaces of horn core pedicels	66·4	61·3
Width across lateral edges of supraorbital pits	–	30·0

Anteroposterior and mediolateral diameters at the base of horn cores of *A. recki*, followed by their length, are:

DK I BM(NH) M 22360	34·9 × 25·0
THC I 068/6659	32·7 × 24·9
FLK I G.229	32·4 × 26·7, length 153·0
FLKN I 1307	34·7 × 23·3, length 140·0
FLKN I 6334	30·2 × 23·7, length 140·0
FLKN I 7266	33·4 × 27·9, length 140·0
FLKN I 067/250	31·5 × 23·3, length 153·0
VEK I BM(NH) M 21462	33·8 × 25·6
VEK I BM(NH) M 21457	33·7 × 24·8
KK I 309	30·9 × 22·1
Bed I BM(NH) M 14509	30·2 × 21·5
Bed I BM(NH) M 14511	31·2 × –
Bed I BM(NH) M 14512	30·1 × 21·2
Bed I BM(NH) M 22363	33·4 × 26·3
HWK II 471	31·2 × 24·6
HWK II 472	22·3 × 16·3
HWK II 568	32·4 × 25·5, length 140·0
HWK East II 278	24·8 × 20·8, length 133·0
HWK EE II 2780	30·9 × 21·3, length 137·0
HWK EE II 3108	25·1 × 17·5, length 119·0
Long K West II 068/6657	30·4 × 24·0, length 140·0
VEK II surface BM(NH) M 21456	34·0 × 29·0
FLK II BM(NH) M 22362	17·8 × 14·9
BK II 1955.71	32·5 × 25·9
VEK IV BM(NH) M 14563	38·1 × 28·2

Measurements on an associated maxilla and mandible of *A. recki* from FLKN I are:

Maxilla 7266		Mandible 7284	
Occlusal length M^1–M^3	36·3	Occlusal length M_1–M_3	39·9
Occlusal length M^2	13·6	Occlusal length M_2	12·6
Occlusal length P^2–P^4	21·0	Occlusal length P_2–P_4	–

These belong to the same individual as the horn core FLKN I 7266 whose measurements are given above.

Measurements on four maxillae of *A. recki* from FLKN I are:

	627	7555	10286	1662
Occlusal length M^1–M^3	38·4	40·1	37·6	46·8
Occlusal length M^2	13·8	14·2	12·1	16·1
Occlusal length P^2–P^4	19·0	–	–	23·4

Maxilla 1662 is rather large and may be another species.

Measurements on 10 mandibles of *A. recki* from FLKN I are:

	Number measured	Mean	Range	Standard deviation	Standard error
Occlusal length M_1–M_3	8 (left + right)	41·8	36·7–46·5	3·6	1·28
	5 (right only)	42·7	39·9–46·0	2·5	1·13
Occlusal length M_2	9 (left + right)	12·8	11·1–14·8	1·3	0·43
	5 (right only)	13·4	11·8–14·8	1·2	0·54

Measurements on mandibles of *A. recki* from FLK I are:

	D.35	B.119	G.154	G.294	G.323	B.492
Occlusal length M_1–M_3	43·5	–	–	42·5	47·2	43·5
Occlusal length M_2	11·7	13·1	13·1	11·9	14·5	11·4
Occlusal length P_2–P_4	–	19·1	18·7	13·2 (P_3–P_4)	–	–

Measurements on two other mandibles of *A. recki* are:

	DK I 261	HWK East II 2103
Occlusal length M_1–M_3	42·8	42·5
Occlusal length M_2	13·7	12·9
Occlusal length P_2–P_4	19·5	–

Immature mandibles FLKN I 231, FLKN I 1310 and FLKN I 7828 have deciduous P_2–P_4 measuring 22·5, 26·7 and 27·2 mm respectively.

Measurements on 16 metatarsals assigned to *A. recki* from FLKN I are:

	Number measured	Mean	Range	Standard deviation	Standard error
Length	16 (left + right)	164	152–185	7·3	1·84
	9 (left only)	163	152–185	9·6	3·21
Least thickness	16 (left + right)	11·5	10·3–12·8	0·5	0·14
	9 (left only)	11·3	10·3–11·7	0·5	0·15

Measurements on 19 metacarpals assigned to *A. recki* from FLKN I are:

	Number measured	Mean	Range	Standard deviation	Standard error
Length	19 (left + right)	161	153–168	4·2	0·98
	13 (left only)	161	153–168	4·2	1·17
Least thickness	19 (left + right)	12·9	11·6–15·1	0·8	0·19
	13 (left only)	13·0	11·6–15·1	0·8	0·22

Measurements of length and least thickness on other limb bones assigned to *A. recki* are:

Femora	DK I 3330	162×15·4	DK I 5385	178×16·0		
Tibiae	DK I 4366	205×14·5	FLK I 9	211×16·4	FLK I F.161	206×15·7
	FLKN I 157	193×14·5	FLKN I 1246	199×15·6	HWK East II 2010	202×16·3
Metatarsal	DK I 3292	165×10·9				
Humeri	FLKN I 8191	130×14·4	FLKN I 10263	130×15·1		
Radii	FLKN I 50	141×18·1	FLKN I 70	138×16·8	FLKN I 666	146×16·3
	FLKN I 682	144×17·9	FLKN I 1300	134×16·2	FLKN I 1605	131×16·0
	FLKN I 8179	137×16·6	BK II 1963.3037	157×16·6		
Metacarpal	FLKNN I 649	162×11·7				

Associated tibia FLKN I 8264 194×14·2 and metatarsal FLKN I 8263 161×11·3 mm.

COMPARISONS. Four Laetolil horn cores in Berlin of *Gazella hennigi* Dietrich (1950: 25; pl. 1, figs 1–2) agree in size and morphology with the shorter horn cores of *Antidorcas recki* (see p. 429 above). They differ from those of the common *G. janenschi* Dietrich (1950: 25; pl. 2, fig. 22) by tapering more quickly, curving back more strongly and diverging quite strongly in their upper parts. The horn core from the Garussi water course is uncompressed, but two from Gadjingero, 45 and 3.39, and one from the Vogel River labelled 'Vo 330 *G.* sp. cf. *capricornis*', are compressed. Dietrich's illustration of the right horn core 45 from Gadjingero is slightly larger than life size.

Scarce horn cores and dentitions from the Shungura Formation, Omo, are of *A. recki* or its progenitor. The horn cores come from levels above Tuff F and differ from the Olduvai Bed I horn cores by a less sharp bending backwards of their distal part, but they do show a flattened lateral surface, transverse ridges and lack of increased divergence in the distal part. An *Antidorcas* mandible is known from member B, but other dental remains are limited to member G. The Omo mandible referred to *Antidorcas* sp. by Arambourg (1947: 390; pl. 30, fig. 3) is most probably an alcelaphine, as has been mentioned on p. 420.

The right and left horn core bases at Peninj, A67.256 and A67.257 (WN64.113), mentioned on p. 429 above, are also *A. recki*. Both sides of a complete upper dentition A67.274 (WN64.300B.2 PT 3.USC), part of a right mandible A67.280 (WN64.241.TMG S.5.?BSC), part of a left mandible A67.296 (WN64.95.MMG.BSC), a left lower molar A67.315 (WN64.152.RDG.S) and a deciduous left P_4 A67.281 (WN64.291.PP.USC) may be the same species. There is no evidence for more than one *Antidorcas* species at Peninj (cf. Gentry *in* Isaac 1967: 254).

At Kanjera the left horn core BM(NH) M 15862, already mentioned, represents *A. recki*. It was identified as *Phenacotragus recki* by Hopwood (*in* Kent 1942: 126). A distal left tibia M 22500 and distal left humerus M 22499 could also belong to *A. recki*.

Several Elandsfontein fossils agree with the *Antidorcas recki* horn cores from Bed I in the transverse ridges on the front surface and lack of increased divergence in the upper parts, but lack a flattened lateral surface and are less mediolaterally compressed. These fossils are a frontlet 8542, right horn core 1195, left horn core 20587 and part of a horn core 6750. They differ from living *A. marsupialis* horn cores in having transverse ridges, no increased divergence in their distal parts, and the backward bend being closer to the base.

Other fossil *Antidorcas* at southern African sites, however, are not conspecific with the east African *A. recki*. Almost certainly to be included in *Antidorcas* is *Gazella bondi* Cooke & Wells (1951 : 207, fig. 3) founded on material from Chelmer, Rhodesia, with an immature row of left upper teeth as holotype. The teeth were smaller than those of impala, had strong styles and were extremely hypsodont. Similar small and very hypsodont teeth from Vlakkraal had been referred to *Antilope* gen. et sp. indet. by Wells, Cooke & Malan (1942 : 217), and Cooke (*in* Mason 1962 : 452) listed the species for Middle Stone Age levels of the Cave of Hearths. Three mandibles at Florisbad (all numbered C.1473) and a large number of isolated teeth are apparently of this species and have typically antilopine moderate-sized to large back lobes on M_3, a springbok-like short premolar row with even P_3 suffering reduction, and a mandibular ramus deepening considerably under the molars. Like the type specimen from Chelmer, all these *bondi* remains are of immature animals. Nevertheless, the immature mandibles of the SHK II herd of *A. recki* definitely have less hypsodont teeth than '*Gazella*' *bondi*, and we would regard this difference in tooth development as more reliable than insubstantial variations in horn core morphology. Vrba (1973) has published an account of cranial remains of *A. bondi* from Swartkrans. The horn cores from this site are less mediolaterally compressed than in other *Antidorcas*, diverging more at the base than higher up and with a tendency to an anticlockwise torsion on the right side, and without a sharp backward bend in their course. The supraorbital pits are rather large for an *Antidorcas*. Despite these very distinctive features, the cranial and basioccipital characters are very like *A. recki* (Vrba 1973 : 290). Vrba also draws attention to some further interesting tooth characters: the lower molars having little flattening of their medial walls, their central cavities with transverse constrictions in the middle, the small occlusal area of the cheek teeth (figs 2, 6) and the extreme shortness of the premolar row (fig. 7). It is unlikely that *A. bondi* was ancestral to *A. marsupialis*. Further discoveries may allow us to know whether its horn core morphology was as variable as that of *A. recki*.

The holotype of *Gazella wellsi* Cooke (1949 : 38, fig. 11) is a left mandible F262 from the Vaal River gravels of Power's site. It is housed in the Department of Archaeology, University of Witwatersrand, Johannesburg. It remains questionable whether this name-bearing mandible is conspecific with *A. recki* or with *A. bondi*, but the stability of the older name *A. recki* will not be affected. Measurements on this mandible are:

Occlusal length M_1–M_3 43·6 occlusal length M_2 13·3

An interesting springbok, *Antidorcas australis*, was described from Swartklip, Cape Province (Hendey & Hendey 1968 : 56, pls 3–4; Hendey 1974 : 52). There are several complete and partial crania and dentitions, which differ markedly from the living springbok by having smaller horn cores which are more mediolaterally compressed and which lack the sharp bending backwards and outwards shortly above the base. They thus have some resemblance to the much smaller female horn cores of living springbok. The dentitions at Swartklip are also smaller. *A. australis* has been recorded from Melkbos (Hendey 1968 : 111), and is also known from Elandsfontein by frontlets 8860, 12214A, 20564 and many horn cores—far more than of *A. recki* at that site. Hendey (1974 : 52) believes that *A. recki* may have been more a species of inland plateaux, and that it is a more likely ancestor for *A. marsupialis* than is *A. australis*. Vrba (1973 : 300) has assigned some Swartkrans horn cores to *A. australis*, and believes that some Swartkrans dental remains are conspecific.

Horn cores of *Antidorcas marsupialis* are known from Florisbad (C.1459 A and B, C.1469), and there are a few springbok-like teeth larger than those of *A. bondi* at the site. One wonders if they come from the same low level as the rest of the fauna and particularly the *A. bondi*.

Antidorcas, or a closely related genus, has been claimed to occur in the north African

Plate 38 (Scales marked in centimetres)

Antidorcas sp. Lateral and dorsal views of frontlet, HEB East IV 1969.814.

Villafranchian-equivalent deposits of Ain Brimba, Tunisia, and Ain Boucherit and Oued el Atteuch, Algeria (Arambourg & Coque 1958 : 612; Coppens 1971 : 53). Bayle (1854) had earlier referred to what may be the same species from Mansoura, Algeria.

Leakey (*in* Clark 1959 : 230) identified as *Litocranius* sp. most of a poorly preserved right tibia BM(NH) M 12150, and proximal and distal right femoral pieces M 12843 and M 12844, from Broken Hill, Zambia. In the more or less central position of the longitudinal digital flexor ridge on its posterior surface the tibia is unlike some species of *Gazella* but does not appear to be especially characteristic of *Litocranius*. The extent of the cnemial crest and its pronouncedly concave lateral surface suggest *Antidorcas* or *Gazella* rather than *Litocranius*. The two femoral pieces are definitely antilopine, but the pit for the origin of the lateral femorotibial ligament can be clearly seen: it is absent in *Litocranius*. The rounded top edge of the great trochanter of the proximal femur may be more like *Litocranius*, but the extent to which this feature may have arisen from superficial damage is uncertain. An unregistered antilopine distal end of a metacarpal, not mentioned by Leakey, has the small indentations above the condyles on the anterior surface probably too deep for *Litocranius*. M 12872 is the distal end of a left antilopine humerus. Although the identification of all these small limb bones is not secure, they seem more likely to indicate *Antidorcas* or *Gazella* than *Litocranius*.

Antidorcas sp.

An *Antidorcas* frontlet from Bed IV with complete right and nearly complete left horn cores and the dorsal parts of both orbital rims, HEB East 814 found in 1969 (Pl. 38), differs from Bed II fossils of *A. recki* in being a little larger, and in having horn cores which bend backwards less strongly and nearer the base and are less mediolaterally compressed. It could belong to *A. recki*, which is represented in Bed IV, or it could be an early *A. marsupialis*. Further finds from Bed IV will be necessary before coming to a decision.

The measurements of this specimen are:

Length of horn core along its front edge	200·0
Anteroposterior diameter of horn core at its base	37·4
Mediolateral diameter of horn core at its base	30·6
Minimum width across lateral surfaces of horn core pedicels	71·7
Width across lateral edges of supraorbital pits	*c.* 39·0

Genus ***GAZELLA*** Blainville 1816

TYPE SPECIES. *Gazella dorcas* (Linnaeus 1758).

GENERIC DIAGNOSIS. Horn cores subcircular or elliptical in cross-section, with some mediolateral compression, the lateral surface often flatter than the medial, fairly uprightly inserted with backward curvature in side view, generally more obliquely set in females than in males of the same species, slightly divergent in anterior view, without keels or torsion; frontals without or almost without internal sinuses and the area between the horn core bases hardly raised above the level of the top of the orbital rims; moderately large triangular supraorbital pits at the base of the horn core pedicels slightly medial to the anteriormost edge of the pedicels; ethmoidal fissure present; moderate to large preorbital fossae; premaxillae generally contacting the sides of the nasals which have shortened during evolution; occipital low with each half often facing partly laterally as well as backwards; moderate to large auditory bullae; living species with hypsodont teeth but less hypsodont in earlier fossil species; upper molars with moderately prominent styles and little development of ribs between them; lower molars without goat folds; M_3s often with the rearmost (third) lobe greatly enlarged; except in the east Asian subgenus *Procapra*, P_4s are without metaconid–paraconid fusion to form a complete medial wall at the front of the tooth.

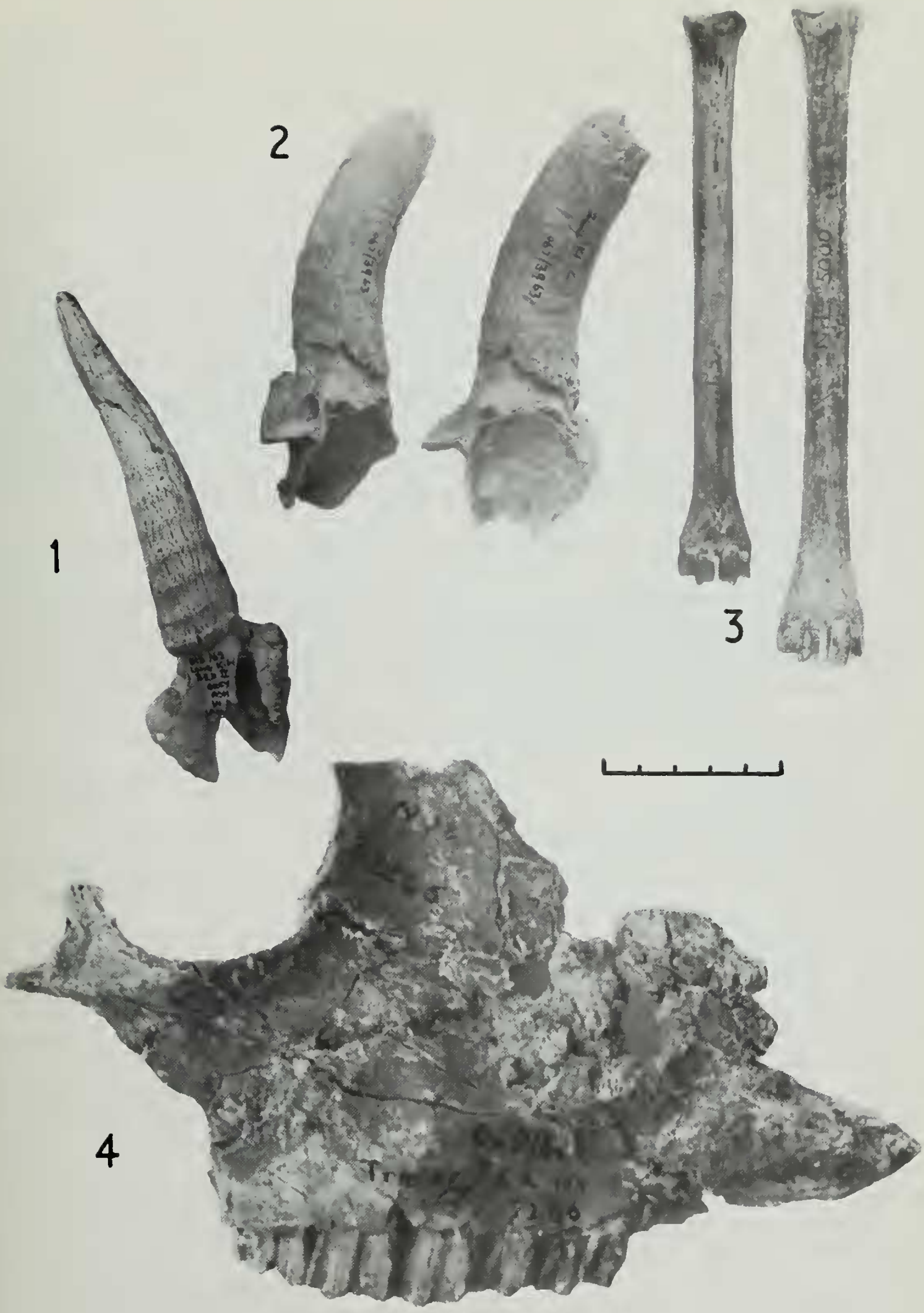


Plate 39 (Scale = 50 mm for Figs 1–3 and 25 mm for Fig. 4)

Antilopini

Fig. 1 ***Antidorcas recki.*** Anterior view of right horn core, Long K West II 1962.068/6657.

Fig. 2 **Antilopini** sp. 1. Anterior and lateral views of left horn core, DK I Surface 1962.067/3963.

Fig. 3 Anterior views of left metatarsals, FLKN I 9372 (left) and FLKN I 5000 (right).

Fig. 4 ***Antidorcas recki.*** Right side of face, FLKN I 7266, to show the preorbital fossa.

Gazella sp.

Gentry (1966 : 64–67) arranged the *Gazella* horn cores from Olduvai in two groups: (1) SHK II 1953.285, BK II 1955.218+226, a tip KK II 1959.224, BM(NH) M 14507 from Bed I, and two female horn cores KK I 1959.310 and BM(NH) M 22362 from FLK II all showed little mediolateral compression; (2) M 14508 from Bed I was more compressed.

A few additional *Gazella* have now come to light. These are the base of a right horn core EF-HR 1963.199 with the frontal, midfrontal suture, supraorbital pit and damaged orbital rim from middle Bed II, an incomplete right horn core FC West 1963.201 with the top of the orbital rim, supraorbital pit and postcornual fossa also from middle Bed II, a complete right horn core HWK EE 1972.2396 with the midfrontal suture, supraorbital pit, postcornual fossa and damaged orbital rim from lower middle Bed II, a left horn core base BM(NH) M 26929 collected in 1931 possibly from Bed I, and a right horn core 068/6695 with the orbital rim and midfrontal suture. Mrs M. D. Leakey (personal communication) thought that the last fossil might come from Bed I and have adherent matrix from a later deposit. R. L. Hay (personal communication, September 1973) wrote: 'The matrix is a slightly clayey quartzose sandstone with a few percent each of augite and altered volcanic glass of probable original basaltic composition. This is a common type of sandstone throughout the western exposures (Main Gorge, west of FLK) of Bed II above the disconformity at the top of the Lemuta Member. This type of sandstone is rare in any other stratigraphic unit at Olduvai.'

It can be seen from the measurements and Fig. 34 that the extent of mediolateral compression in Olduvai *Gazella* horn cores is greater than can be expected in a single species, but that M 14508 is scarcely more compressed than M 14507, FC West 201 or HWK EE 2396. The last is very like the middle and upper Bed II horn cores but thinner mediolaterally. We now take the horn cores as being of one unnamed species, with M 14508 only doubtfully included. The female horn core M 22362 has internally hollowed frontals and can no longer be accepted as belonging to *Gazella*

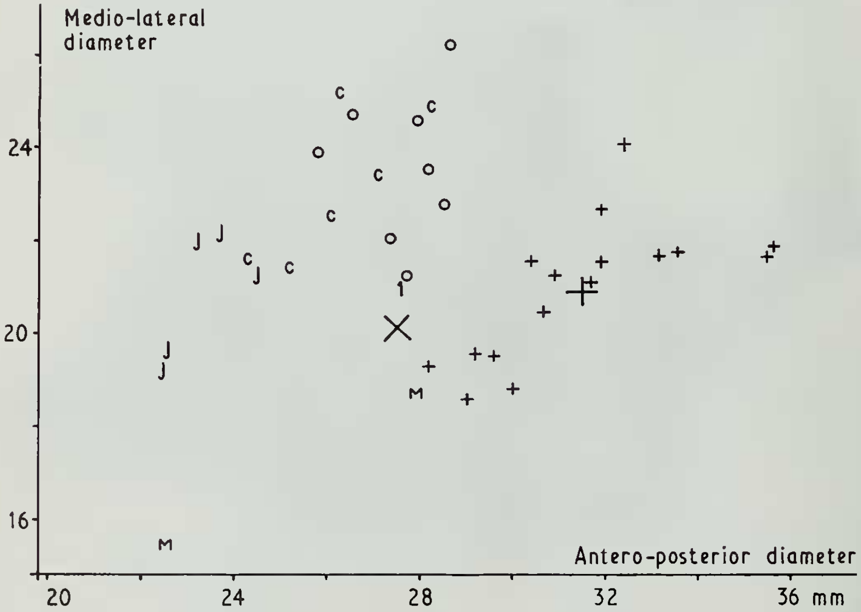


Fig. 34 Horn core dimensions of gazelles.

O = *Gazella* sp. from Olduvai and Peninj, C = same species from Elandsfontein, J = *Gazella janenschi* from Laetolil, M = *G. praethomsoni* from the Shungura Formation, 1 = BM(NH) M 14508; the adjacent circle is *Gazella* sp. HWK EE 2396, + = *G. thomsoni*, with a large + indicating the mean reading, large X = mean for 13 *G. dorcas*.

(see p. 429). The remaining horn cores can be described as moderately long, slightly divergent, inserted rather obliquely, only a little curved backwards, without transverse ridges, having a flattened lateral surface, often with deep longitudinal grooving anteriorly and posteriorly, and having the greatest mediolateral diameter situated nearly centrally on the cross-section. The postcornual fossae are variably deep, as in living gazelles, but often more strongly localized. There is no internal hollowing of the frontals at the horn core bases, and the level of the frontals between the horn cores is no higher than the orbital rims.

The gazelle mandibles SHK II 1957.793, BK II 1952.152 and a surface find from MLK II in 1955 can also be placed in this species, as was done by Gentry (1966 : 66). We can thus be sure that a gazelle with little-compressed horn cores occurs in Olduvai middle and upper Bed II. It probably also occurs in Bed I, but at that time its horn cores were a little more compressed.

Leakey (1965 : 64) provisionally used the name *Gazella praecursor* Schwarz for the horn cores M 14507 and M 14508. Schwarz (1937 : 41 ; pl. 2, figs 4–5) had founded *G. gazella praecursor* on Olduvai material, which was destroyed in the Second World War. Unfortunately he figured only a tibia and a cervical vertebra, and described the horn cores as very compressed, parallel proximally but diverging outwardly in their upper parts, and with the upper parts strongly bent backwards. To us this reads more like a description of *Antidorcas recki* than of *Gazella* horn cores, although we have not taken the step of formally listing *G. g. praecursor* as one of the synonyms of that species. We believe the name *G. g. praecursor* should be dropped from use.

Measurements. Anteroposterior and mediolateral diameters at the base of the gazelle horn cores are:

Bed I BM(NH) M 14507	27·4 × 22·0	HWK EE II 1972.2396	27·7 × 21·2
Bed I BM(NH) M 14508	27·6 × 21·0	SHK II 1953.285	28·7 × 26·2
Bed I? BM(NH) M 26929	28·0 × 24·6	BK II 1955.218 + 226	26·6 × 24·7
FC West II 1963.201	28·6 × 22·8	068/6695	28·2 × 23·5

The length along the front edge of SHK II 1953.285 is 160·0, and of HWK EE II 1972.2396 153·0 mm.

Measurements on the gazelle mandibles are:

	SHK II 1957.793	BK II 1952.132
Occlusal length M_1–M_3	40·4	–
Occlusal length M_2	13·0	13·2
Occlusal length P_4	9·6	–

Comparisons. The gazelle of Olduvai middle and upper Bed II is represented at Elandsfontein by a number of horn cores, including 9473. Some very small straight ones are the females, for example 3783, 12753 and 16522. Some mandibles, for example 2855 with a complete row of cheek teeth, can also be attributed to the species. The only other site from which we know the species is Peninj, on the evidence of the right horn core A67.248 (WN64.75 MMG/N). The anteroposterior and mediolateral diameters at the base of this horn core are 25·8 × 23·9 mm.

This Olduvai, Elandsfontein and Peninj gazelle differs from both *G. dorcas* and *G. thomsoni* in its less compressed horn cores and relatively longer premolar rows. However, the level of the greatest mediolateral diameter lies more anteriorly on the cross-section than in *G. dorcas* and this does not differ from *G. rufifrons* and *G. thomsoni*. The low inclination of the horn cores is a further resemblance to the two latter species, so we may tentatively align the fossil species more closely with them than with *G. dorcas*.

Among named fossil forms *G. praethomsoni* Arambourg (1947 : 387; pl. 32, figs 4, 4a) from Omo is characterized by extreme mediolateral compression of the horn core, and is certainly a distinct species from the Olduvai middle and upper Bed II gazelle. A second and larger horn core, L.35–35, was found in 1968 in member G of the Shungura Formation. A still larger and strongly curved complete horn core, B.377 from the Brown Sands locality of the Usno Formation, may also be the same species. It seems likely that these horn cores represent a different lineage from the Olduvai gazelle, and did not evolve into that species by lessening their horn core compression.

Despite Arambourg's choice of a specific name and the mediolateral compression of its horn cores, *G. praethomsoni* need not be ancestral to *G. thomsoni*. The closest relative of the latter must surely be the west African *G. rufifrons* with its less compressed horn cores, and this makes the Olduvai gazelle equally available as an ancestor. The mandible which Arambourg (1947: pl. 27, figs 1, 1a and 1b) assigned to *G. praethomsoni* is from an antilopine, perhaps *Antidorcas*.

Another named African fossil gazelle is *G. gracilior* Wells & Cooke (1956 : 37; pls 20–21) from Makapansgat Limeworks. The holotype frontlet BPI M.773 was described as the male of a small slender-horned gazelle, but the small horn cores set so widely apart suggest that it could equally well be the female of a larger species. The London specimen figured by Wells & Cooke, BM(NH) E.5775 (Anthropology collection), is more robustly horned but the postcornual fossa lies somewhat laterally to the horn core base instead of being tucked up near it as would be normal in a male gazelle, which suggests that this fossil is also a small-horned, presumably female example of a larger species. The braincase wall behind the horn core projects quite a long way laterally. The lack of any flattening of the lateral surface of the horn core or of deep longitudinal grooving anteriorly or posteriorly, and the smooth texture of the surface are also compatible with it being a female. The mandibles assigned to *G. gracilior* (BPI M.766, M.767, M.768 and M.771) by Wells & Cooke are all rather large. In fact, all the *G. gracilior* material from Makapansgat Limeworks probably belongs to *G. vanhoepeni* (see p. 443).

A multitude of specific names already exists for north African fossil gazelles. Arambourg (1957) has brought some order to those of the upper Pleistocene, but his final opinions on the Pliocene and earlier Pleistocene ones have yet to appear. It can be accepted that a gazelle for which *G. atlantica* Bourguignat (1870: 84; pl. 10, figs 14–15) is the correct name was abundant in the middle and later Pleistocene of Barbary. It was moderately large, about the size of a springbok, and had rather short and thick horn cores showing little mediolateral compression, strong backward curvature and a flattened lateral surface. The supraorbital pits were sometimes large, and the basioccipital of a male cranium seen by A. W. Gentry in Paris some years ago had poorly marked anterior tuberosities situated closer together than in living gazelles. Despite its short and backwardly-curved horn cores *G. atlantica* is probably not related to *G. dama* because it is no bigger than contemporaneous fossils of *G. cuvieri*, whereas *G. dama* is a much bigger species. On the other hand *G. dorcas* is rather small to be descended from *G. atlantica*. Bate (1940 : 419, 429) described gazelles of a size close to *G. atlantica* from the early Holocene of Palestine. For the present the identity of these gazelles is best left open, and we may merely note that the Olduvai gazelle is unlikely to be *G. atlantica* on account of its smaller size, longer horn cores with weaker backward curvature, and perhaps the smaller supraorbital pits.

G. tingitana Arambourg (1957 : 68; pl. 1, figs 1–4; pl. 2, figs 6, 8) is a late Pleistocene north African species having long slender horns like the living *G. leptoceros* but more backwardly curved. Other middle and later Pleistocene fossils from this area can be assigned to living species, so none are like the Olduvai gazelle.

Two names exist for north African horn cores of an age equivalent to the Villafranchian. One is *G. setifensis* (Pomel 1895 : 15; pl. 10, figs 14–15), and the other *G. thomasi* (Pomel 1895 : 18, a renaming of '*G. atlantica*' Thomas 1884 : 17; pl. 1, fig. 9). The holotype of *G. thomasi* is a right horn core base, mistakenly shown as a left in Thomas's illustration, which is very small and possibly from a young animal. Its basal anteroposterior and mediolateral diameters are 21·2 × 14·7 mm. It thus shows strong mediolateral compression like the Omo *G. praethomsoni*, as was discussed by Arambourg (1947 : 389–390). *G. setifensis* is larger, and is less compressed and more curved.

Plate 40 (Scale = 50 mm for Figs 1–5 and 25 mm for Fig. 6)

Fig. 1 **Alcelaphini** sp. 3. Anterior view of left horn core, SHK II 1953.280.

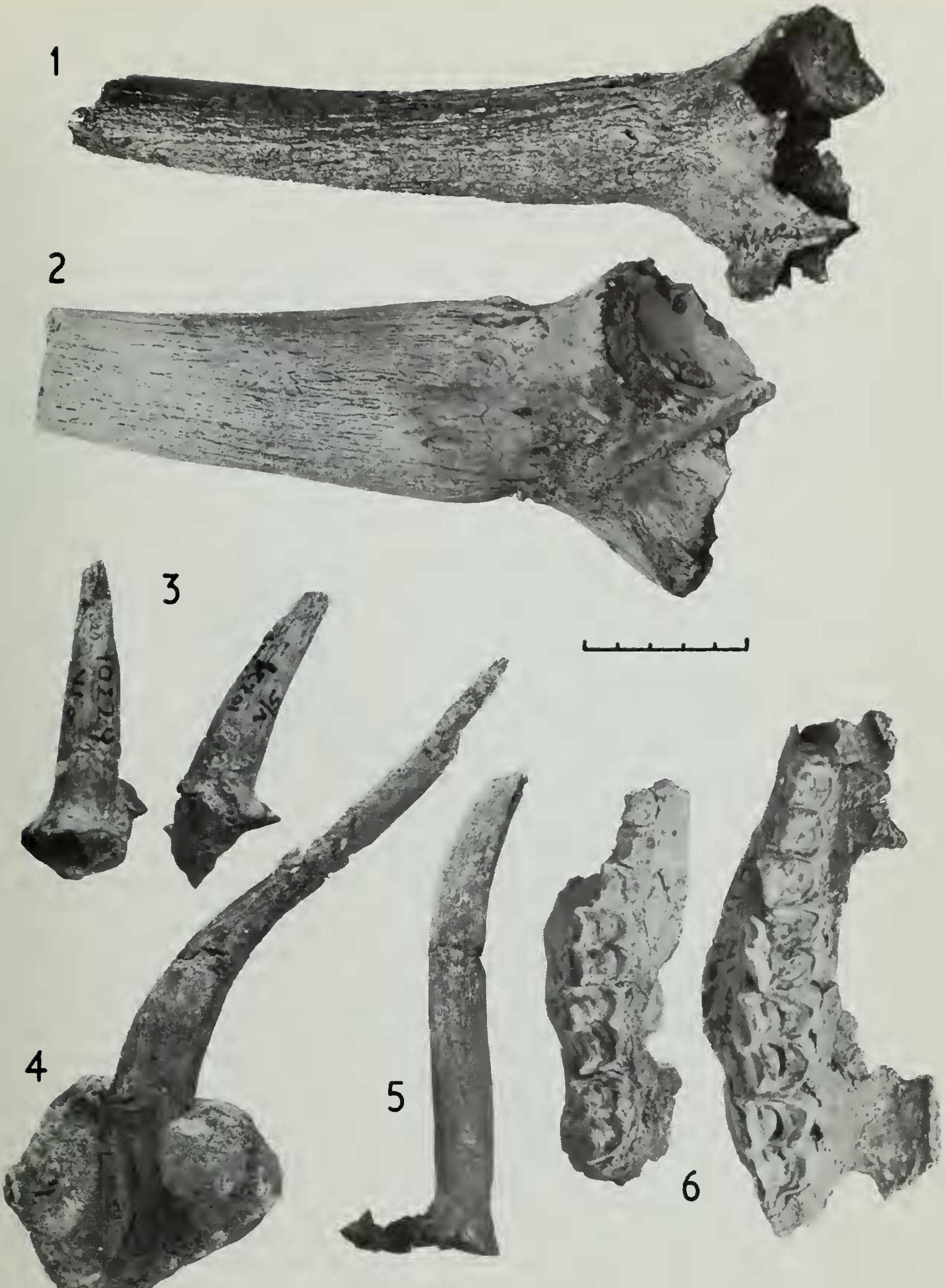
Fig. 2 **Alcelaphini** sp. 3. Lateral view of right horn core, F 3000.

Fig. 3 ? **Neotragini** indet. Two views of horn core, FLKN I 10229.

Fig. 4 **Alcelaphini** sp. 4. Horn core, FLKN I 7884.

Fig. 5 **Alcelaphini** sp. 4. Horn core, FLKN I 5196.

Fig. 6 ***Antidorcas recki***. Right P^2–M^3 of FLKN I 1152 (on the left) and of FLKN I 1662 (on the right).


1
2
3
4
5
6

Its basal anteroposterior and mediolateral diameters are given as 38 and 24 mm, which is larger than in the Olduvai gazelle.

One of the three gazelles from Laetolil named by Dietrich may be close to the Olduvai gazelle despite the greater antiquity of the Laetolil fauna. There are four right and six left nearly complete horn cores in Berlin of *G. janenschi* Dietrich (1950 : 25; pl. 2, fig. 22) from the Vogel River, Gadjingero, Deturi and Garussi water courses. The illustrated left horn core from Garussi is almost complete and has preserved the supraorbital pit, midfrontal and parietofrontal sutures. The horn core is moderately long, very little compressed, inserted obliquely and close to the midfrontal suture, curves a little backwards and lacks a flattened lateral surface, keels or transverse ridges. In anterior view its slight outward divergence lessens towards the very tip. It has deep longitudinal grooving posteriorly, a deep and localized postcornual fossa, and there is extremely little hollowing of the frontals. The specimen can be eliminated from the Reduncini by the narrow and rather drawn-out triangular supraorbital pit, and in any case small reduncine teeth are lacking in all Laetolil collections.

Horn cores similar to those of *G. janenschi* in the London Laetolil collection are an almost complete left horn core BM(NH) M 22483, incomplete right horn core M 22493, basal half of left horn core M 22491, and parts of horn cores M 22494 and M 22484. In Nairobi are the bases of left horn cores 1959.46 and 1959.50, bases of right horn cores 1959.48 and 1959.49, and the basal half of a right horn core MUG (Mugheim) 1, of which 1959.49 and 1959.50 are the best preserved. The crushed skull in Berlin (Dietrich 1950 : pl. 5, fig. 52) is probably a female of *G. janenschi* as Dietrich suggested. It has extremely worn teeth. BM(NH) M 22491 and M 22493, and 1959.49 and 1959.50 in Nairobi, have more internal hollowing of the frontals, more flattening of the lateral surface, and perhaps greater initial divergence than in the other specimens.

G. janenschi differs from the Olduvai gazelle in having horn cores less thickened at the base, divergence lessening slightly towards the tip, no flattening of the lateral surface and more backwards curvature. In the absence of any contrary evidence, it is possible that *G. janenschi* could be ancestral to the Olduvai, Peninj and Elandsfontein gazelle.

There seems little reason to separate the maxillae assigned by Dietrich to '*Gazella hennigi*' (1950 : pl. 5, fig. 47) from the teeth and mandibles assigned to *G. janenschi* (pl. 2, figs 14–15; pl. 5, fig. 48); the *G. janenschi* 'maxillae' of pl. 5, fig. 48 are single teeth, on the large side, which have been mounted together in plaster. Such teeth and dentitions are smaller than those of *Antidorcas recki*. Similar antilopine teeth and dentitions are in the London Laetolil collection. These are partial left mandibles BM(NH) M 15110 and two numbered M 22488, two right mandibles numbered M 22486 and two numbered M 22487, right M_3 in fragment of mandible M 26784, right M^1+P^4 M 22485, left upper molars M 22485, M 22495 and one without number. Comparable remains in Nairobi are a complete left lower dentition 1959.603 + 605, partial left lower dentition 1959.143, partial right lower dentitions 1959.152 and 1959.296 + 298, right maxilla with two molars 1959.452, right upper molars 1959.308, 1959.319, 1959.320 and 1964. no number, left upper molar 1959.321, and four right lower molars without number found in 1959. The mandibles in London all show that the ramus below the teeth is shallow, as in the Olduvai *Gazella* mandibles SHK II 1957.793 and BK II 1952.152, and the M_3s have enlarged back lobes.

Two incomplete Laetolil left mandibular pieces have rami too deep for them to belong with the other specimens. They are 1959.54 in Nairobi which is in two parts with M_2 and M_3 on one part and P_2 and P_3 on the other, and M 29428 in London with the back of deciduous P_4, M_1 and M_2. The P_2 of 1959.54 is very small. Possibly these fossils represent *Antidorcas*.

The teeth assigned to *Gazella kohllarseni* by Dietrich (1950 : 25; pl. 2, fig. 16; pl. 5, fig. 49), all three 'tooth rows' consisting of single teeth mounted in plaster, appear antilopine, are larger than the teeth of *G. janenschi* and must belong to another species. Similar remains are present among the London Laetolil material (e.g. partial left mandible M 22487 and a left lower molar M 22488) and in Nairobi (incomplete left mandibles 1959.150, 1959.294 and 1959.443 + 444, left lower molar 1959.168, left upper molar 1959.315 and right upper molar 1959.625). These fossils are the same size as or still larger than the large antilopine maxilla 1662 from Olduvai FLKN I and some single teeth from FLK I and FLKN I. Some of them may belong to relatively recently fossilized *G. granti* (see p. 293).

The left horn core from Garussi called *G. kohllarseni* by Dietrich (1950 : 25; pl. 1, fig. 7) is unlikely to belong in the Antilopini (see p. 351).

A left horn core BM(NH) M 15883 from Kanam West, with basal diameters of 32·2 and 22·8 mm, is larger than the Olduvai gazelle but agrees in the rather anterior level of the maximum mediolateral diameter.

A fuller picture of the evolution of gazelles in Africa south of the Sahara can only emerge from the finding of much more complete specimens than we have at present. It is very doubtful if one can get a reliable story by considering only the degree of mediolateral compression of the horn cores. The conclusions which can be made at present about gazelles are as follows. African fossil gazelles are known back to the late Miocene (Gentry 1970a : 293). Their range has extended at times to the southernmost tip of the continent, although nowadays they go no further south than Tanzania. The Olduvai gazelle from middle and upper Bed II is conspecific with the gazelle at Elandsfontein; it could well have been the ancestor of the extant *G. thomsoni* and *G. rufifrons*, and may itself be descended from the Laetolil *G. janenschi*. The Omo *G. praethomsoni* is different from the Olduvai middle and upper Bed II gazelle and may represent a different lineage. It may not be different from some of the supposedly earlier Olduvai horn cores, especially BM(NH) M 14508, which are only provisionally considered conspecific with the later Olduvai ones. There is more definite evidence for a second lineage of gazelles which will be considered under the next heading.

Fossil remains of larger gazelles

Schwarz (1937 : 53; pl. 2, figs 6–7) referred to *Gazella granti* a radius, two ulnae and three metatarsals from Olduvai, but this material has not survived the Second World War. One of the ulnae and the radius were illustrated, but the photographs do not show any characters whereby the bones can be identified. Therefore we have not included *G. granti* on the Olduvai list.

The base of a right horn core of *G. granti*, 1959.236, is present in the Laetolil collection at Nairobi. It is less mineralized than other Laetolil fossils, and is most likely to be of late Pleistocene or Recent age. Dietrich (1950 : 27) also referred to *G. granti* in the younger deposits at Laetolil. Pieces of a probable right horn core BM(NH) M 15851 + M 25627 and a left one M 15851 from Kanjera could belong to *G. granti*. M 15883 from Kanam is smaller but similar.

The horn core from Karungu M 22502 said by Gentry (1966 : 104) to resemble *G. granti* now looks to us more like a Recent and scarcely fossilized *G. thomsoni*.

The remains of a large gazelle from Makapansgat Limeworks were first described by Wells & Cooke (1956 : 43, figs 22–24) as *Phenacotragus vanhoepeni* but have now been correctly referred to *Gazella* by Wells (1969b : 162). The horn cores of this species are moderately long, strongly compressed with a flattened lateral surface, without keels or transverse ridges, inserted rather uprightly above the orbits and moderately far apart. They bend sharply backwards half-way along their length and are nearly parallel except for slightly increased divergence towards their tips. Some features seen on the crania are the rather wide orbital rims, small to moderate preorbital fossae, only a slight central indentation of the parietofrontals' suture, a prominent median occipital ridge with poor flanking hollows, large mastoids, fairly large auditory bullae, small foramina ovalia and little transverse constriction on the basioccipital.

Wells (1969b : 162) has already mentioned that *G. vanhoepeni* could belong with the group of large living gazelles comprising *G. granti*, *G. soemmerringi* and *G. dama*. Indeed in several characters it is plausible as an ancestor for *G. granti*; these are the uprightly inserted and mediolaterally compressed horn cores, a fairly long braincase, deep postcornual fossae, a complicated and raised midfrontals suture, moderate-sized but not large supraorbital pits and large anterior tuberosities of the basioccipital.

G. gracilior from Makapansgat Limeworks is probably conspecific with *G. vanhoepeni* as discussed previously on p. 440. The horn cores assigned to this name are likely to be the females of *G. vanhoepeni*, and they are a little bigger relative to those of the males than in living gazelles. *G. vanhoepeni* would therefore be characterized by rather poor sexual dimorphism of its horns.

Vrba (1973 : 309 footnote) has made the tentative suggestion that *G. gracilior* may turn out to be an *Antidorcas*, but we prefer to maintain our existing opinion.

Gazelle horn cores from Langebaanweg (L.3491, L.6077, L.6078, L.9149 and L.10694) are mediolaterally compressed and curve backwards quite strongly. They are large for their geological age (Pliocene), and could be ancestral to *G. vanhoepeni*.

Genus INDETERMINATE

Antilopini sp. 1

A number of small horn cores from Olduvai can perhaps be placed in the Antilopini. These are

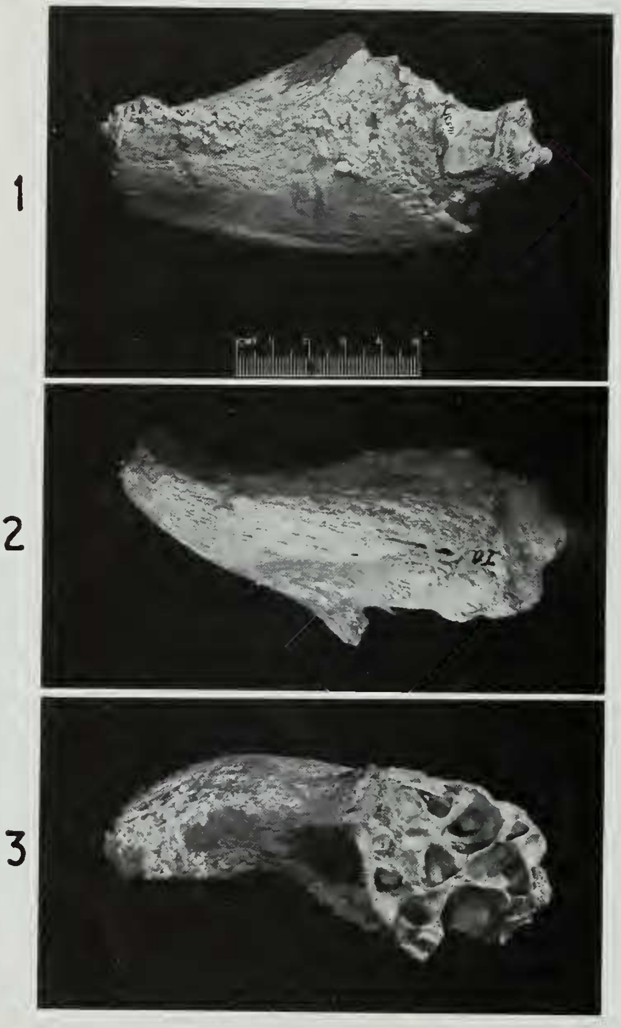


Plate 41 (Scale marked in cm and mm)

? Caprinae sp.

Fig. 1 Supposed dorsal view of right horn core from Bed I, BM(NH) M 14531.

Fig. 2 Supposed anterior view of same horn core.

Fig. 3 Supposed posterior view of same horn core.

the basal half of a left horn core with the midfrontal suture and supraorbital pit 1962.067/3963 (Pl. 39, fig. 2) and the basal part of a left horn core 1962.067/3965, both from the surface of DK I, the basal part of a left horn core with the midfrontal suture and supraorbital pit MNK II 1963 .2818, the basal part of a left horn core with the midfrontal suture, supraorbital pit and top of the orbital rim BK II 1955.63, the base of a right horn core BK II 1957.991, and the basal part of a left horn core BM(NH) M 22364. The horn cores are a little compressed mediolaterally, without a flattened lateral surface, with a slight approach to a posterolateral keel, inserted on short pedicels above the orbits, inserted fairly uprightly in side view, almost parallel at the very base in front view but with rapidly increasing divergence above, with a small and moderately deep postcornual fossa, no internal hollowing of the frontals, frontals between the horn core bases not raised above the level of the top of the orbital rims, and fairly large triangular supraorbital pits.

Most of these characters would fit *Gazella* very well, but the lack of any flattening of the lateral surface, the more upright insertions, and the rapidly increasing divergence above the base are differences from the other gazelle horn cores from Olduvai. Moreover the definite Olduvai *Gazella* is represented at BK II alongside this species, and appears to be no different in size. If both species are really antilopine, perhaps one was comparable in way of life to the living *Litocranius walleri*. One might wonder about uniting this species with Alcelaphini sp. 4, but at present it still seems that the latter is distinguished in its internally hollowed horn core pedicel, slightly greater mediolateral compression, and stronger spiralling. It is also likely to be an earlier species than Antilopini sp. 1.

Measurements. Anteroposterior and mediolateral diameters at the base of these horn cores are:

DK I 1962.067/3963	27·6 × 24·2	BK II 1957.991	28·4 × 22·6
MNK II 1963.2818	31·7 × 24·0	BM(NH) M 22364	25·7 × 20·0
BK II 1955.63	31·4 × 24·9		

Comparisons. Three horn cores from the Shungura Formation at Omo, F203-32 and F203-103 from member K and F356-10a from member L, appear conspecific with the Olduvai horn cores.

Subfamily CAPRINAE

This is basically a Eurasian subfamily, living members of which occur also in North America and on the fringes of the Palaearctic faunal realm in Africa. Two early African bovids from Fort Ternan have been assigned to the Caprinae (Gentry 1970a : 262, 284) on the basis of their very close resemblance to their Eurasian contemporaries. There is slender evidence for supposing that later members of these lineages evolved into Alcelaphini (Gentry 1970a : 315), and that living Caprinae and their fossil relatives evolved in Eurasia (Gentry 1971). However, it is now known that at least one (Gentry 1970b) and probably two species of the caprine tribe Ovibovini have in the past inhabited regions of Africa remote from the Palaearctic.

Makapania broomi Wells & Cooke (1956 : 26) from Makapansgat Limeworks has been assigned by Gentry (1970b) to the Ovibovini, and appears to be very similar to the European Villafranchian *Megalovis latifrons* Schaub.

It also seems likely that a second ovibovine lineage has inhabited Africa. BM(NH) M 14531 (Pl. 41) is a small horn core with part of the frontal found in Olduvai Bed I in 1932. It tapers quickly from a wide compressed base, and curves in two planes. There are no keels or transverse ridges. A small surface concavity can be seen on what is likely to be the ventral side. Part of the frontal's surface medial to the horn core base seems to lie on the vertical plane and must certainly be at an angle to the rest of the skull roof. The broken frontal shows an extensive system of small sinuses quite unlike the large sinuses of Alcelaphini, but similar to those which occur in Ovibovini and Bovini. The plane of the frontals shows that the horn core cannot be from a small *Syncerus*. This rather mysterious horn core shows some resemblance to the frontlet of '*Bos*' *makapaani* Broom (1937 : 510, figured) described from a cave 'near Makapaansgat, about 10 miles from Pietpotgieters Rust' which later became known as Buffalo Cave (Cooke 1952 : 33). There is reason to suppose, from the likely position of the sutures, that the convex edges of the horn cores on Broom's frontlet are anterior or anterodorsal and not posterior. This would give it some resemblance to *Budorcas taxicolor* Hodgson, the living takin of Tibet and western China. Possible ovibovine remains also occur at other sites, for example three teeth in members C, D and G of the Shungura Formation, Omo.

Three caprine-like metapodials have also been excavated from Bed I. A right metatarsal 067/1009 from FLKN I level 3, a left metatarsal 068/6665 from levels 1-3, and a left metacarpal 9394 from level 5 which was referred to the Caprini by Leakey (1965 : 68(a)), are complete and are very short (Pl. 19, fig. 2). The metatarsal 068/6665 has low distal condyles with outside edges not parallel and poor distal flanges on the anterior surface. However, it cannot be tragelaphine because the rear naviculocuboid facet is strongly pointed upwards at the back. The anterior central groove is not markedly deep, but the hollows flanking the distal condyles are deep. The posterior surface is not hollowed. The second metatarsal is slightly longer and thinner. Measurements of length and least thickness on these metatarsals are:

FLKN I 068/6665 167 × 23·8 FLKN I 067/1009 173 × 20·2

The metacarpal has a magnum–trapezoid facet which lacks a protuberance on its medial side. The unciform facet is relatively larger than in Alcelaphini, and it has no posterolateral projection nor an anterolateral angled edge. This limb bone measures 175 × 24·9 mm.

The distal ends of these metapodials are rather like small Bovini but the proximal ends are not. They are similar to goats in the rather poor distal flanges on the anterior surface, the not very upcurved ectocuneiform facet in side view, the longitudinal groove on the metatarsal front, the anteroposterior compression of the whole bone, the shortness and the low distal condyles.

The distal end of a left tibia FLKN I 7243 from levels 1–2 may belong with the metapodials. The posterior edge of the articular facet is very little indented centrally and the size would agree with the metapodials.

Continued in Part II, published as *Bull. Br. Mus. nat. Hist.* (Geol.) **30** (1).